

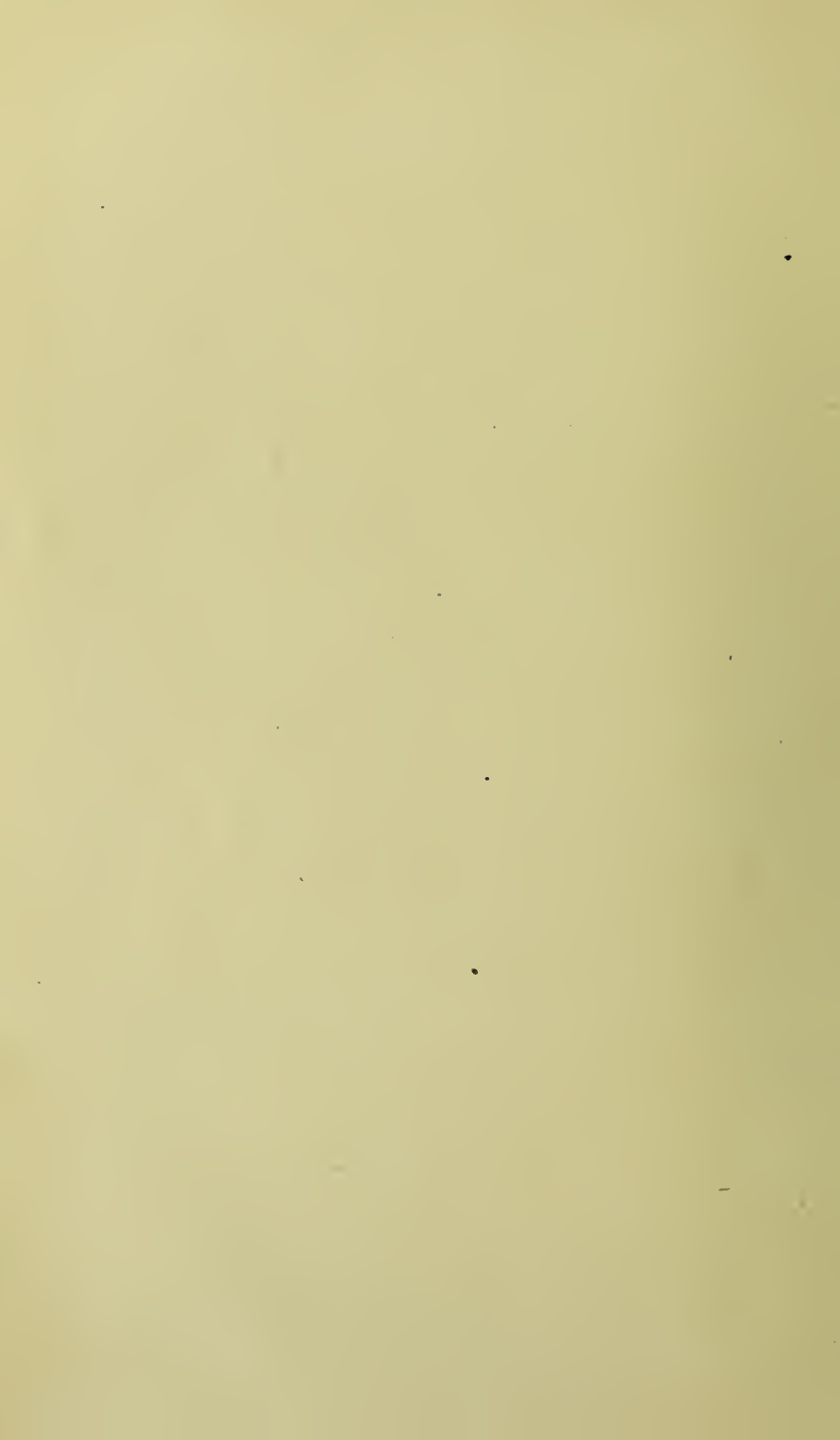




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A STUDENT'S TEXT-BOOK OF ZOOLOGY

## CORRIGENDA

- Page 9. Line 7. For "chordate" read "non-chordate."
- „ 16. Line 6. Omit "mesodermal."
- „ 17. In the description of fig. 6, for "spina" read "spinal."
- „ 117. Line 5. For "branchia" read "branchial."
- „ 125. Line 8. For "Myliobates" read "Myliobatis."
- „ 146. Line 8. For "somactido" read "somactids."
- „ 152. Line 13. The genus *Odontaspis* is not extinct, see line 1 of the same page.
- „ 210. Line 15 from bottom. For "*Gastrosteus*" read "*Gasterosteus*."
- „ 219. Line 4. For "*vulggaris*" read "*vulgaris*."
- „ 219. Line 20. For "E. Ind. *Oreinus*; McClell" read "E. Ind.; *Oreinus* McClell,
- „ 220. Line 12. For "RHODENIA" read "RHODENA."
- „ 229. Line 26. For "trumpetor" read "trumpet or."
- „ 230. Line 13. Insert a comma after "Raf."
- „ 231. Line 6 from bottom. Omit "*Seriolella*."
- „ 235. Line 18. For "specie" read "species."
- „ 242. Line 27. Insert comma after *Elanura*, and another after *Melletes*.
- „ 242. Line 11-12 from bottom. The 5th letter of the word *Stellerina* is indistinct.
- „ 244. Line 23. For "*Thallasso*-" read "*Thalasso*."
- „ 255. Line 14 from bottom. For "succus" read "saccus."
- „ 273. In the second footnote for "Paratoids" read "Parotoids."
- x) „ 276. Line 13 from bottom. Insert after the words "in other Amphibia." "In *Rana* the ductus endolymphaticus which passes off from the sacculle enters the cranial cavity through the foramen endolymphaticum and there dilates into the saccus endolymphaticus. This extends back into the neural canal of the vertebral column, where it lies in close apposition to its fellow along the dorsal side of the spinal cord and gives off transverse diverticula which end in small dilations over the posterior root ganglia. The fluid contained in the saccus and its extensions is milk-white, the milkiness being due to the presence of crystals of carbonate of lime (otoliths). The CALCAREOUS GLANDS are the terminal dilations of the transverse diverticula above referred to (see Gaup, *op. cit.*, p. 261). The function of this peculiar extension of the membranous labyrinth is unknown (for a somewhat similar condition in the *Ascalabota*, see p. 323).
- „ 237. Line 12. The word "is" has dropped out.
- „ 315. Line 10 from bottom. For "*Trimatosaurus*" read "*Trematosaurus*."
- „ 334. Line 21. For "*phenodon*" read "*Sphenodon*."
- „ 393. Line 6. For "*lon ifrons*" read "*longifrons*."
- „ 400. In description of Fig. 221. For "*(Pariasaurus)*" read "*(Pariasaurus)*."
- „ 412. Line 3 from bottom. For "Sectional" read "Section 1."
- „ 459. The footnote is referred to on line 1 of p. 460.
- „ 465. Line 25. For "*M. gallopavo*" read "*Meleagris gallopavo*."
- „ 473. Line 8 from bottom. Delete "*Picoides*."
- „ 475. Line 21. For "*M. superba*" read "*Menura superba*."
- „ 582. Line 21. After "birth;" insert "Dicotyles Cuv,"
- „ „ Line 7 from bottom. For "H" read "Hippopotamus,"
- „ 653. For "Order 21," read "Order 22"
- „ 655. Line 16, for "pectora" read "pectoral."

C. A. HOARE.

# A STUDENT'S TEXT-BOOK OF ZOOLOGY

BY  
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## PREFACE

IN presenting the second part of my work on Zoology to the public I must apologise for the delay in its appearance and for the fact that I am not keeping to the undertaking which I gave in the preface to my first volume that the work would be completed in two volumes. The delay in publication has been caused in part at least by the fact that the Vertebrata compel a lengthier and more detailed treatment than the other groups. Not only is more known about them, but they excite greater interest, and their palaeontological history has been more completely worked out than in the case of any other phylum. The result has been the present bulky volume which deals only with them and with Amphioxus.

Embryology is of course excluded, except in the case of Amphioxus, but I have endeavoured to deal fairly fully with anatomy, habits, and classification. In the systematic portions I have probably been too ambitious, but the usefulness of a book of this kind depends largely upon its completeness in this respect, and in cases of doubt I have generally included rather than excluded. In Aves alone have I made a selection; for there are many excellent works devoted to them and it would be impossible to give anything like a complete list of their genera.

In judging the anatomical portions I would ask the reader to remember that this is not exclusively a work on Comparative Anatomy, and limitations of space forbid an exhaustive treatment. This branch of the subject has not, however, been neglected, and questions of general interest have usually been at least touched upon.

Considerable space has been given to extinct forms.

As in the first volume I have endeavoured in the index to refer the reader to the page on which technical terms are defined and most of the abbreviations are explained in the same place.

To Mr. J. J. Lister, F.R.S., I am again under very great obligations. He has looked through all the proof sheets and has given me the full benefit of his wide knowledge and great critical powers. I am also indebted to his pencil for the excellent illustrations on p. 341 and p. 532.

My thanks are also due to Professor Newton, Professor Ray Lankester, Mr. Boulenger, Professor MacBride, Professor Graham Kerr, Dr. Chalmers Mitchell, Dr. Andrews, Mr. Walter Heape, Mr. Assheton, Dr. Gaskell, Dr. Marett Tims and others for the assistance they have given me in different parts of the work.

My principal sources of information are acknowledged in the footnotes, but I must not omit to mention here works from which I have obtained special help ; these are Gadow's *Amphibia and Reptiles* and Evans' *Aves* in the *Cambridge Natural History*, Flower and Lydekker's work on *Mammalia Living and Extinct*, Smith Woodward's *Outlines of Vertebrate Palaeontology* and Zittel's *Grundriss der Palaeontologie*, and Gunther's *Introduction to the Study of Fishes*. The excellent volume on fishes in the *Cambridge Natural History* and Weber's great work on the *Säugethiere* appeared too late to be utilised.

Of the illustrations about fifty are new ; of the remainder a considerable number are from Claus' *Lehrbuch*, but some, of which I have been permitted to make use by the courtesy of the author and publisher, are from Smith Woodward's *Vertebrate Palaeontology*, Reynold's *Vertebrate Skeleton*, Flower and Lydekker's *Mammalia Living and Extinct*, Flower's *Osteology of Mammalia*, Huxley's *Anatomy of Vertebrate Animals*, Shipley and MacBride's *Zoology*, Zittel's *Grundzüge der Palaeontologie*, Korschelt and Heider's *Text Book of Embryology*, Gegenbaur's *Vergleichende Anatomie der Wirbelthiere*, Wiedersheim's *Grundriss der Anatomie der Wirbelthiere*, Perrier's *Traité de Zoologie*,



Balfour's *Comparative Embryology*, Gadow's *Amphibia and Reptiles*.

The third volume, which is in the press, will deal with the Tunicata, Enteropneusta, Echinodermata and Arthropoda.

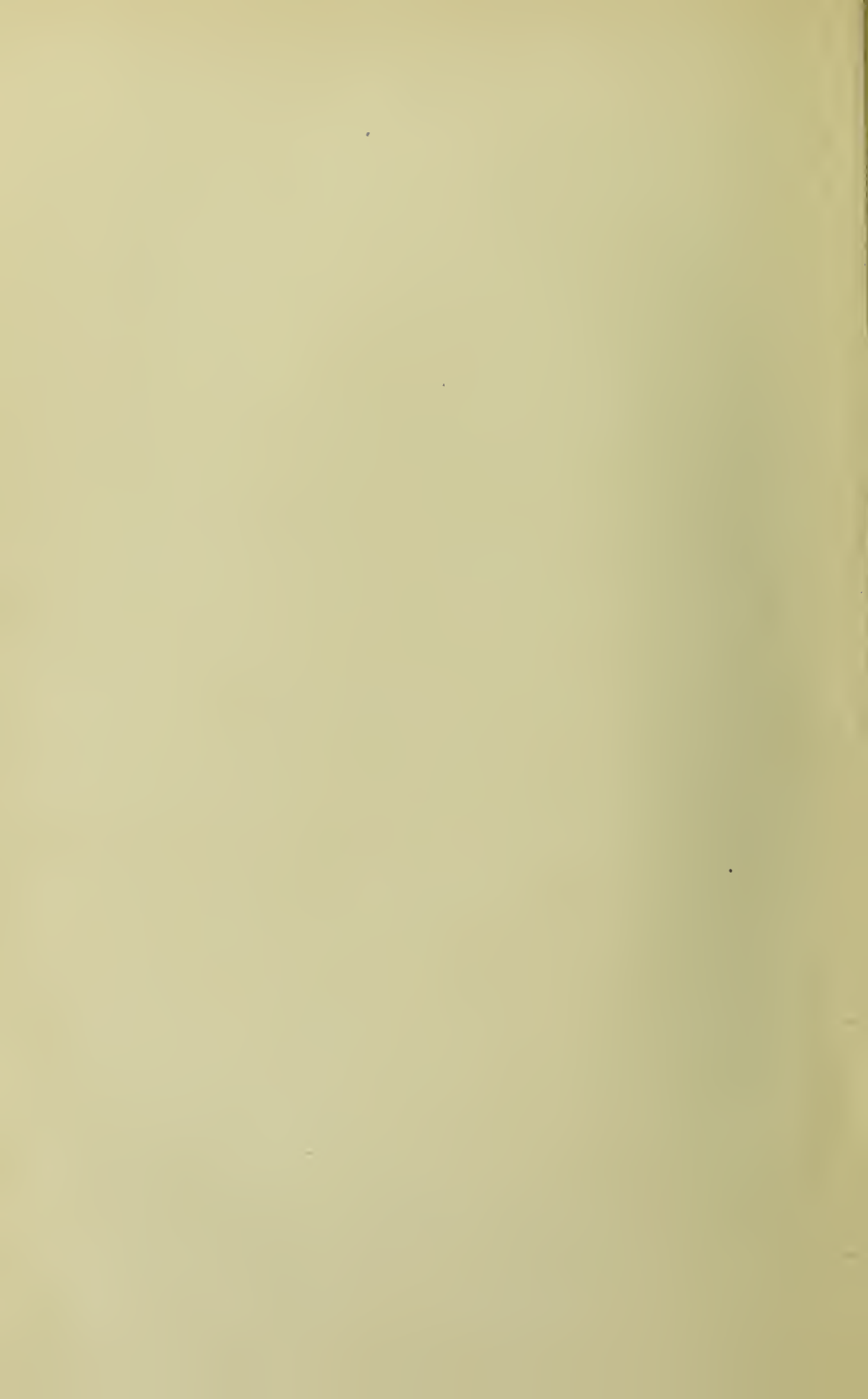
It has been pointed out to me by friends who have read the proofs that I have made statements which without a fuller treatment may give rise to the view that I am unorthodox on the great question of organic evolution. This is not the place to give that fuller treatment, but in order to prevent misunderstandings I may say that any such view would be erroneous. I am and always have been a convinced evolutionist. I hold, that is to say, that matter is constantly undergoing change, and that natural selection, taking advantage of its endless diversity in form and properties, has played and is playing an important part in determining what form of it (whether living or non-living) shall exist and what shall cease to exist. I hold further that the forms of living matter, as well as those of non-living matter, owe their existence and their properties to the operation of natural laws, though here we are treading on more uncertain ground, for we know nothing of the origin of living matter or of the sources of its properties. The chemist has made many forms of matter which have, at present at least, no existence in nature apart from organisms, but he has not yet succeeded in making living matter. Whether he will ever be able to do so is a question which may fairly be asked, but is one which cannot now be answered. The view that living matter arose in response to the operations of natural laws cannot be either proved or disproved. It must remain a matter of belief for which there is much to be said. As to the origin of the manifold properties of living matter we know nothing. The Darwinian theory did not account for properties; it left their origin to an imperfectly understood interaction between the organism and the environment, and further than this we cannot at present go. It may, however, be pointed out that there are two ways in which

this great question may be attacked. One of these is by the method of experiment—a method which is being pursued with increasing vigour by more than one school of Biologists ; the other is the careful and thorough examination of living and extinct organisms, particularly in their relations to one another. It is the second of these methods which comes under our notice in the three volumes of the first part of this work dealing with systematic zoology. It is unquestionable that this study does shed light, if only a dim light, on the course of organic evolution and indirectly on the origin of the properties of living matter, and it is most important that the light so obtained should be brought to bear upon the problem. To discover this we must approach the subject with unbiassed minds, for it is one of immense complexity and it is extremely unlikely that any particular solution which commends itself to us will turn out to be final. I would therefore ask for lenient judgment if in some pages of this work I have seemed to take up an unduly critical position with regard to views widely prevalent at the present time on some aspects of organic evolution. That does not mean that I am unsound on the great question itself, but only that I am sceptical as to the value of some hypotheses widely held as to the course of organic evolution. It is true that working hypotheses are necessary in constructive work, but in a subject of the complexity of the present one, they can only be provisional and as such are legitimately open to criticism. It may be urged that I have said too much or too little, that I ought not to have touched upon the matter unless I was prepared to state fully my own views. While allowing that there would be some justice in such a criticism, I do not admit its complete validity. In deference to it, however, I have materially altered in proof what I had written in manuscript, but it was not possible to remove all reference to the subject. It was necessary to note the facts in passing. In the final volume on the Principles of Zoology which I yet hope to write, I shall return to it and endeavour to justify, in the fuller treatment which will there be pos-

sible, the criticisms which are only hinted at here. At the same time I cannot hope to build. That is the task of the great band of workers in many departments of Biology, who, undeterred by failure and urged on by the fire, enthusiasm, and generous aspirations of youth, return time after time, generation after generation, to the assault of the fortresses of nature well knowing that their material reward will be small, that defeat means the world's neglect and that success, except the greatest, brings but a pittance of its esteem. To them I inscribe this book in the hope that it may serve if only to a small extent to smooth over the difficulties of part of the road which at first they have to traverse.

A. SEDGWICK.

TRINITY COLLEGE, CAMBRIDGE,  
*February, 1905.*



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An asterisk signifies that the group is extinct.

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# TABLE OF GEOLOGICAL PERIODS AND FORMATIONS

## TERTIARY OR CAINOZOIC PERIOD.

<b>Pleistocene</b>	Recent Deposits. Valley and Cave Deposits Glacial Deposits.
<b>Pliocene</b>	Cromer Beds. Norwich Crag. Red Crag. Coralline Crag. In India, the Siwalik Formation.
<b>Miocene</b>	Not known in Britain but wide-spread on the Continent of Europe. Lacustrine deposits of North America { Loup Fork. Deep River. John Day. The Santa Cruz Beds of Patagonia are referred to the Miocene.
<b>Oligocene</b>	Hamstead and Bembridge Beds. Headon and Osborne Beds. In N. America the freshwater White River Beds belong to the Oligocene.
<b>Eocene</b>	Upper: Barton Beds; In N. America, Uinta Group. Middle: Bracklesham Beds. In N. America, Bridger Group. Lower: Bagshot Sands, London Clay, Woolwich and Reading Beds. In N. America { 1. Wind River Group. 2. Wasatch Group. 3. Torrejon Group. 4. Puerco Group.



## SECONDARY OR MESOZOIC PERIOD.

Cretaceous	{	Upper	{	Upper Chalk (with flints).
			{	Middle Chalk (with few flints).
		Lower	{	Lower Chalk.
			{	Upper Greensand.
			{	Gault.
Jurassic	{	Upper	{	Lower Greensand.
			{	Wealden.
		Middle	{	Purbeck and Portland Beds.
			{	Kimmeridge Clay (Solenhofen Slates in Bavaria.)
			{	Corallian and Oxford Clay.
Triassic	{	Upper	{	Great Oolite.
			{	Inferior Oolite (Stonesfield Slate belongs here).
		Lower	{	Upper Lias.
			{	Middle Lias.
			{	Lower Lias.
Triassic	{	Upper	{	Rhaetic Beds.
			{	Keuper Marls and Sandstone.
		Middle	{	Muschelkalk, absent in Britain.
			{	Lower: Bunter Sandstone, Pebble Beds, Karoo of S Africa.
			{	

## PRIMARY OR PALAEOZOIC PERIOD.

Permian . . .	{ Upper : Magnesian Limestone. Lower : Red Sandstones.
Carboniferous . .	{ Upper { Coal Measures. { Millstone Grit. Lower : Carboniferous Limestone and Shales.
Devonian . . .	{ Upper Old Red Sandstone. Limestones (marine). Lower Old Red Sandstone.
Silurian . . .	{ Ludlow. Wenlock. May Hill Sandstone (Llandovery).
Upper Cambrian*	{ Bala. Llandilo, Arenig.
Lower Cambrian .	{ Tremadoc Series. Lingula Flags. Menevian Series. Harlech Series. Olenellus Beds.
Precambrian .	

\* L. Silurian of Murchison, Ordovician of Lapworth.



## CHAPTER I.

# CHORDATA.

*Animals with a notochord, a hollow dorsally placed nervous system, and a pharynx opening to the exterior by lateral passages.*

The group Chordata is a division of the animal kingdom superior to a phylum. It includes four phyla and is to be compared in its rank to such groups as the *Metazoa* and *Coelomata*, both of which are phylum-including divisions. The four phyla into which the group Chordata is divided are, stating them in the order in which they are dealt with in this work, the *Cephalochorda*, which includes but a single genus, *Amphioxus*; the *Vertebrata*, which is by far the largest and most important division of the group; the *Tunicata*, which includes a considerable number of marine forms of low organization; and lastly the *Enteropneusta*, which has but a small number of genera mainly of vermiform appearance and is the most outlying phylum of the group. Indeed, by some highly competent authorities the Enteropneusta are placed altogether outside the Chordata, largely on account of their early development, which differs in important particulars from that of other Chordata and approaches that of Echinodermata; and because it is not certain that they possess that typically chordate organ, the notochord. While not presuming to pronounce an opinion on the latter point beyond saying that if the notochord is present in Enteropneusta, its development, structure and relations to other organs differ considerably from those of the notochord in the other phyla, we desire to emphasise quite distinctly our opinion that the Enteropneusta are Chordates. They present most clearly the other characteristic features of that group, viz., the hollow central nervous system and the perforated pharyngeal wall—features of organization found in no other group of the

animal kingdom ; and in the arrangement of their coelom they come close to the Cephalochorda and Vertebrata.

The notochord itself is a rod-like structure in all cases developed from the dorsomedian endoderm of the embryonic enteron. This streak of tissue undergoes a modification of structure almost identical with that presented by the axial endoderm of the tentacles of many Coelenterata. The modification, which may be described as being of a skeletal nature, consists in both cases of a vacuolisation of the protoplasm of the

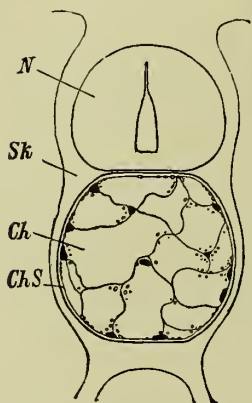


FIG. 1.—Transverse section through notochord and spinal cord of the larva of *Bombinator igneus* (after Götze, from Claus). *ChS* notochordal sheath; *Ch* notochord; *Sk* skeletogenous layer; *N* spinal cord.

endodermal tissue (Fig. 1) and of a considerable development within this tissue of cuticular structures (vide Vol. i, p. 101). Indeed the function of the notochord, like that of the tentacular endoderm referred to, is a supporting one: it supports the axis of the body and particularly the central nervous system beneath which it lies. In the Cephalochorda this function is discharged by the notochord during the whole of life; in the Vertebrata and Tunicata however it is purely embryonic or larval in its duration.

In the Vertebrata the notochord, though it may in some forms, e.g. Pisces, persist throughout the whole of life, becomes surrounded by a stiff sheath, which takes over its function of

axial support and becomes, especially in those forms in which the endoskeleton acquires rigid texture, divided up into segments corresponding with those of the embryonic muscular system. The central nervous system develops from the ectoderm of what is usually called the dorsal surface, and at first nearly always has the form of a groove, which, excepting in the Enteropneusta, extends along the whole of the dorsal surface and closes completely to form a canal—the central canal of the nervous system. It is characteristic of Cephalochorda, Vertebrata and Tunicata that this canal opens in the embryo for a shorter or longer period unto the enteron (neurenteric canal). This neurenteric communication is however never maintained in

the adult, and its transitory existence is a highly remarkable fact for which no satisfactory explanation has ever been offered. In the Enteropneusta alone is the central nervous system confined to a short portion only of the dorsal surface (so-called collar region), and in them alone does the central canal remain permanently open and never acquire a communication with the enteron.

We have said that the central nervous system arises on the dorsal surface. Now it is quite clear that this surface corresponds to the ventral surface of other Coelomata, so that it would be convenient to exchange the term dorsal for a term which would include the same surface in all Coelomata. Such a term is afforded by the term *neural surface*, which implies, and correctly implies, that the central nervous system is developed upon it. Another term, *blastoporal*, having reference to the position of the embryonic blastopore might also be used. In all the Coelomata the blastopore is not only placed on the neural surface of the body, but actually perforates the embryonic rudiment of the central nervous system. This is seen most clearly in the embryonic history of the Cephalochorda, the Vertebrata, the Annelida, Arthropoda and Mollusca. In the Enteropneusta and Echinodermata this relation is masked, and by many morphologists would be held not to occur at all. But that it does exist we are convinced, and is a most important morphological fact appertaining to all Coelomata. Now in some Coelomata it has been definitely proved that the mouth and anus of the adult animal are directly derived from the embryonic blastopore, and it becomes a question whether this derivation, though not embryonically manifested in all forms, does not also hold throughout the Coelomata. Believing as we do in the homology of the mouth and anus, at least in the phyla Annelida, Arthropoda and Mollusca, it follows that this relation holds for them. In *Peripatus* the mouth and anus are not only derived from the elongated blastopore by its constriction into two openings, but remain throughout life included within the nerve ring derived from the neural rudiments of the embryo.\* If in other

\* Sedgwick, "Monograph of the Development of *Peripatus capensis*," *Studies from the Morphological Laboratory of the University of Cambridge*, 4, 1889, p. 1.

Arthropoda, in Annelida and in Mollusca we find, as we do, that the nerve ring referred to is, in the adult, incomplete behind the anus, and that the mouth and anus, though obviously referable to the blastopore, are not actually both derived from it, must we on this account deny this most obvious relation and maintain that the mouth or anus, as the case may be, in these forms is not homologous with that of *Peripatus*?

To maintain such a position appears to us impossible, and we entirely accept the doctrine that the mouth and anus of the Annelida, Arthropoda and Mollusca are both perforations of the embryonic neural surface and are specialisations of parts of one original opening which is represented in most embryos by the blastopore. When however we come to apply this doctrine to the Chordata we stand upon more debatable ground. Placing the Enteropneusta on one side as not obviously conforming to our plan, we find that it is a fact of observation that in the Chordata the blastopore perforates the embryonic nerve rudiment, and that in some of them the anus is directly derived from it (many Pisces, some Amphibia, e.g. newt), whereas in others, not at all remote from these, the blastopore closes entirely and the anus is a new formation (some Pisces and Amphibia, e.g. frog, Amniota). Here also we think it may fairly be maintained that notwithstanding the diversity in the mode of development of the anus it is, in all Vertebrata at least, a derivative of the blastopore. The non-inclusion of the anus within the nerve rudiment in the adult, and its shift on to the ventral surface, cannot be brought against this view, because these facts apply both to animals in which the anus is a persistent part of the blastopore, as well as to those in which it is a new formation. Here again, as in the invertebrate phyla already dealt with in this connection, the anus escapes in the adult from the embryonic nerve rudiment; or to put it in another way the part of the nerve rudiment behind the anus never attains full development, but early undergoes atrophy.\* So far then all is plain sailing, in the Vertebrata at least: the anus is a persistent portion—not the whole, as is clear from a consideration of the development of Elasmobranchs and some Amphibia—of the blastopore, as it is in the invertebrate

\* See especially *Lepidosiren*, in which the medullary folds of the embryo include the blastopore which becomes the anus.



Coelomata; and as in most of the latter the part of the nerve rudiment behind it (in the primitive position, anterior in the position which the anus secondarily acquires on the ventral surface) undergoes atrophy.

We now come to the question of the chordate mouth, a much vexed question, and one about which much of a highly speculative character has been written. We may at once concede

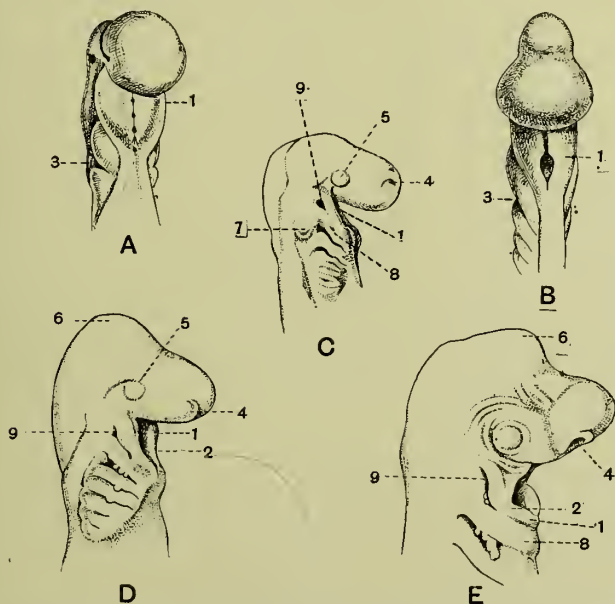


FIG. 2.—Heads of young Elasmobranch embryos (*Scyllium canicula*) (after Sedgwick). A. Ventral view of head of embryo, 7 mm. in length, with two open pharyngeal clefts. The mouth is present as a longitudinal groove in the ectoderm of the buccal depression. B. Same view of a slightly older embryo; the buccal groove has become a longitudinal slit. C. Side view of head of embryo, 9 mm. in length, with three open slits. D. Side view of head of embryo, 11 mm. in length; rudiments of external gills have appeared on the hyoid and on the first and second branchial arches. E. Side view of head of embryo of 16 mm.; external gills have appeared on mandibular arch and the angle of the jaw is marked. 1 mandibular arch; 2 angle of jaw; 3 second pharyngeal cleft; 4 nasal pit; 5 eye; 6, midbrain; 7, auditory sac; 8 hyoid arch; 9 spiracle.

the point that the chordate mouth has never been brought into developmental relation with the blastopore. Even if it be allowed that the chordate blastopore really extends to the front end of the nerve rudiment (medullary plate), which is in itself a disputed point, no morphologist has ever brought to light any embryological fact which is at all in favour of the view that the mouth was originally within the nerve rudiment,

and that its present position outside it and on the ventral surface is a secondary one, due to shifting and to atrophy of the part of the nerve rudiment in front of it. There are a number of features of vertebrate morphology of the highest interest in connection with this point: such are the cranial flexure, the close relation of the infundibulum, which there is good reason to believe is the real front end of the nerve axis, to the anterior end of the mouth, the slit-like form \* (Fig. 2), which at first characterizes the buccal opening, and its extension into the rudiment of the pituitary body; but there is no actually ascertained fact which tends to show that the mouth is a derivate of the blastopore, as it must be conceded to be in most other coelomate phyla. †

The last chordate character to be considered is the possession of lateral pharyngeal apertures. These are often used for respiration and are in consequence generally termed gill-slits. They are not however always respiratory in function—indeed in the majority of the Vertebrata in which they form a very conspicuous feature they are not respiratory at all, but are entirely functionless, being found only in the embryo.

An attempt has been made in some quarters to refer the chordate mouth to a modification of a pair of these structures. We can see no fact in favour of such a view, and we are not prepared to give up the homology of the chordate mouth with that of other Coelomata. We have already stated the case with regard to its relation to the blastopore, and we have seen that there is no good embryological evidence in favour of its being so related, but we do not consider that this absence of evidence is sufficient to put out of court the view that it is the homologue of the mouth of other Coelomata. In many of these, too, no relation can be shown between the mouth and the blastopore in development, but yet we well know that in them the mouth is homologous with the mouth of forms in which it is directly derived from a part of the blastopore.

Finally there is one point in the morphology of the Chordata,

\* Sedgwick, "Notes on Elasmobranch Development," *Q.J.M.S.*, 33, 1892, p. 559.

† For a fuller discussion of these questions, the reader is referred to the article "Embryology" in the recently issued supplement of the *Encyclopaedia Britannica*.



which though not referred to in the definition, is of considerable importance, and must be shortly dealt with here, and that is the form and development of the Coelom. In the Cephalochorda and Enteropneusta the coelom originates as outgrowths of the primitive gut (archenteron). In Vertebrata, though there is no actual outgrowth of the enteron, the walls of the coelom originate from tissue which is derived from the wall of the enteric space, and there can be but little doubt that the mode of development is referable to the enterocoelic type, found in the two other phyla, and is indeed a modification of it.

If then we leave out of consideration the Tunicata, which in this respect cannot at present be brought into line with the other chordate phyla, we may assert that an enterocoelic origin of the coelom, or a modification of it, is characteristic of the Chordata. Outside the Chordata a similar mode of origin of the coelom is found in the Chaetognatha (vol. i, p. 590), in the Brachiopoda (vol. i, p. 580), probably in the Phoronidea (vol. i, p.

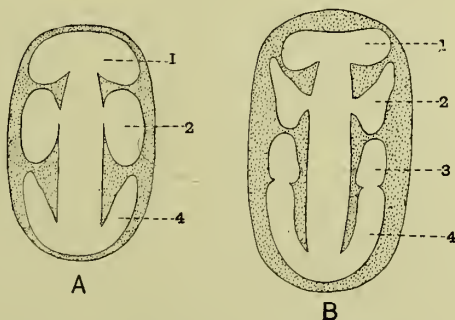


FIG. 3.—Diagrams showing the origin and primitive relations of the coelomic sacs *A* in *Balanoglossus*, *B* in *Amphioxus* (after MacBride). 1 proboscis cavity in *A*, preoral cavity in *B*; 2 collar cavity; 3 anterior somite of trunk; 4 trunk cavity.

546), and as will be shown further on in the Echinodermata. But the coelomic resemblances between these animals go farther than this. In the Enteropneusta the archenteric outgrowths are five in number—two pairs and an anterior unpaired outgrowth (Fig. 3). These, following the nomenclature of Bateson, have been named according to the position they occupy in the adult: the anterior unpaired sac is called the *proboscis cavity*; the sacs of the anterior pair are the *collar cavities*; and the posterior sacs are the *trunk cavities*. In the Enteropneusta they undergo no further division, but remaining in the parts of the body indicated by their names, they give rise to the coelomic spaces of the adult.

In *Amphioxus* the anterior unpaired sac is called the preoral

or head cavity ; it obviously corresponds to the proboscis cavity and remains in the head region of the animal. The sacs of the second pair are called the collar cavities, because they correspond to those cavities of the Enteropneusta. They are in reality the anterior pair of somites, and give rise dorsally to the first pair of myotomes. Their exact disposition in the adult is not quite certain, but they appear to get some backward extension. The posterior sacs which come off as one pair from the enteron and correspond to the trunk cavities of Enteropneusta undergo in subsequent growth a segmentation and give rise to the whole of the mesoblastic somites of the trunk from the second pair backwards.\* In the development and arrangement of its coelomic sacs *Amphioxus* resembles in a remarkable manner the Enteropneusta, the difference between them consisting in the segmentation which the trunk cavities undergo in *Amphioxus*.

In the Vertebrata, though it is not possible to point to such close resemblances as those which we have just described, there is a remarkable similarity in the embryonic arrangement. The first coelomic sac is preoral and unpaired ; the second is paired and large, extending backwards in the mandibular arch, so as to overlap the following somites. These mandibular cavities are clearly homologous with the collar somites of the other types. Following them we find on each side one large cavity, the dorsal parts of which are divided up into segments and become the *myocoel*s, and their walls the *myotomes* of the later embryo. These posterior cavities clearly correspond to the trunk cavities of the other types : as in them they are extensive, and occupy the whole trunk region, and as in *Amphioxus* they are metamerically segmented.

In *Amphioxus* it is said that the preoral somite does not give rise to striated muscles ; in Vertebrata it gives rise to a considerable number of the eye muscles.

With regard to the nonchordate phyla with enterocoelic coelom, we have only space to say this, that in the Echinoderms the Enteropneust plan of an unpaired anterior cavity and two pairs of posterior cavities can, according, to MacBride's researches, generally be made out ; that in the Chaetognatha there is an approximation to the Enteropneust arrangement, but the unpaired

\* MacBride, *Q.J.M.S.*, 40, 1898, p. 589.

cavity is at the hind end ; in the *Phoronidea* there are indications that the Enteropneust arrangement or a modification of it exists, but the indications are not very clear ; while in the Brachiopoda according to our present knowledge no resemblance to the Enteropneust plan exists save in the enterocoelic origin of the coelom.

The formation of the coelom in the other <sup>non-</sup>chordate phyla, the Annelida, the Mollusca, and the Arthropoda, <sup>^</sup> must be regarded as a modification of the enterocoelic method, but it is never possible in them to trace the arrangement into an unpaired chamber and two pairs of chambers which is so characteristic of the Chordata.

## CHAPTER II.

### PHYLUM CEPHALOCHORDA.\*

*With dorsal tubular nerve-cord, and persistent notochord extending forwards in front of the nerve-cord. The muscular system and gonads are segmented, and the pharynx possesses a large number of branchial slits which open into an atrial cavity and are provided with tongue bars. Without paired fins, jaws, brain, vertebrae and generative ducts. The larval life is prolonged and the larva is remarkably asymmetrical.*

The phylum **Cephalochorda** contains but the single genus, *Amphioxus* Yarrell. It was discovered by Pallas in 1778, who took it for a slug and named it *Limax lanceolatus*. Its true position in the animal kingdom was first recognized in 1834 by Costa, by whom it was named *Branchiostoma*. Two years later it was described by Yarrell, who called it *Amphioxus*, by which

\* J. Müller, *Ueber den Bau und die Lebenserscheinungen des Branchiostoma lubricum (Amphioxus lanceolatus)*, Berlin, 1844. Quatrefages, "Sur le système nerveux et sur l'histologie du Branchiostome," *Ann. des Sci. Nat.* (3), 2, 1845. Kowalevsky, "Entwick. v. *Amphioxus lanceolatus*," *Mém. Acad. Imp. Sc.*, St. Petersburg (7), 2, 1867. Id. "Weitere Studien, etc.," *Arch. f. mic. Anat.* 13, 1877. Stieda, "Ueb. d. *Amphioxus lanceolatus*," *Mém. Acad. Imp. Sc.*, Petersburg, (7), 19, 1873. Rolph, "Ueb. d. Bau d. *Amphioxus*," *Morph. Jahrb.* 2, 1876. Langerhans, "Zur Anat. d. *Amphioxus*," *Arch. mic. Anat.*, 12, 1876. A. Schneider, *Anat. u. Entwick. der Wirbelthiere*, Berlin, 1879. Hatschek, "Ueb. d. Entwick. *Amphioxus*," *Arb. a. d. Zool. Inst. Wien*, 4, 1881, also *Zool. Anz.*, 7, 1884, p. 517, and *Anat. Anz.*, 3, 1888, p. 662. Rohon, "Ueb. *Amphioxus lanceolatus*," *Denksch. k. Akad. d. Wissenschaft, Wien*, 45, 1882. Lankester, "Contributions to the knowledge of *Amphioxus lanceolatus*," *Q.J.M.S.*, 29, 1889, p. 364. MacBride, "The Early Development of *Amphioxus*," *Q.J.M.S.*, 40, 1898, p. 589. A. Willey, *Amphioxus, etc.*, New York, 1894, and *Q.J.M.S.*, 31, 1890, p. 445, and 32, 1891, p. 183. v. Wijhe, "Beitr. z. Anat. des Kopfreion des *Amphioxus*," *Petrus Camper*, 1901, and *Anat. Anz.*, 8, 1893. C. F. Cooper, "Cephalochorda," in J. S. Gardiner's *Fauna etc. of Maldive and Laccadive Archipelago*, 1, 1903, p. 347. R. C. Punnett, "Meristic Variation in Cephalochorda," *Ibid.*, p. 361.

name it has since been known. According to the strict rules of zoological nomenclature this is incorrect, the generic name *Branchiostoma* having two years' precedence over *Amphioxus*. But, as so often happens in human affairs, the unwritten law has triumphed over the written, and the almost universal custom of zoologists has been to call the genus *Amphioxus*. From this custom we shall not venture to depart in this work.

Having thus entered our protest against a breach of conventional rule which is made knowingly, we had almost said wantonly, by all zoologists, we may proceed to consider the actual position in the system of this remarkable creature. Here fortunately there is no conflict between preaching and practice, between a pedantic conformity to rule and a lawless adhesion to custom. For law and custom alike agree that the position of an animal in the system shall be determined by its natural affinities as revealed by a study of its structure and development. Judged by this test there can be no question that *Amphioxus* is closely allied to the *Vertebrata* and must be placed either within that group or in close juxtaposition to it. As our readers know we have adopted the latter course and have placed *Amphioxus* in a special phylum of its own, equal in morphological importance but very inferior in the number of its members to the great phylum *Vertebrata*, and have applied to it, out of a number of claimants,\* the name *Cephalochorda*, in allusion to the extension of its notochord into the anterior part of the cephalic region.

*Amphioxus*† is a small, semi-transparent, colourless animal. Its body is elongated, laterally compressed, and pointed at each end; and it may attain a length of two inches. It is entirely marine, and is found at moderate depths in many parts of the world. It has a remarkable power of moving in sand, in which it is usually partially buried, its mouth alone protruding. But it is capable of swimming, and when removed from the sand bends its body with great activity from side to side. The mouth is an elongated oval aperture on the ventral surface immediately behind the anterior end of the body. It is surrounded by a number of delicate ciliated processes, the *oral cirri*.

\* *Pharyngobranchii*, *Acrania*, *Leptocardii*, etc.

† The anatomical description refers, unless otherwise stated, to *A. lanceolatus*.



The anus is also ventral and is placed slightly to the left of the middle line at some little distance from the posterior end of the body (Fig. 5). Extending from the mouth backwards along the ventral surface for about two-thirds of the length of the animal is a wide median groove, bounded by lateral folds and perforated at its hind end by a pore (Fig. 5). The folds are called the *metapleural folds* and the pore the *atrial pore*.

There are no paired fins, but there is a continuous median fin consisting of a fold of skin extending along the whole length of the dorsal surface (dorsal fin), and round the hind end of the body on to the ventral surface as far forwards as the ventral groove (Fig. 4). Anteriorly it is also continued on the ventral surface, reaching as far as the mouth, with the right side of which it is continuous (Fig. 5). The portion between the ventral groove and the anus may be called the *anal fin*, and that between the anus and the hind end of the body the ventral part of the caudal fin.

*Amphioxus* is a segmented animal. The segmentation is marked externally by a number of V-shaped grooves, placed one behind the other on each side of the body, the apex of the V being directed forwards (Fig. 4). These markings are caused by the insertion into the skin of a number of transverse septa of connective tissue, which divide the great lateral longitudinal muscles of the body into a series of successive segments, placed one behind the other and called *myotomes*. The grooves of the two sides of the body alternate with one another. The segmentation is also exhibited by the gonads which consist of a series of saccular bodies extending throughout the greater part of the pharyngeal region as far back as the atrial pore (Fig. 4). They correspond in number with the myotomes of that part of the body in which they occur and alternate with those of the opposite side of the body.

The body of *Amphioxus* is traversed throughout almost its entire length by a flexible skeletal rod—the **notochord**. The notochord is pointed at either end and is placed in the centre of the body, but nearer to the dorsal than the ventral surface (Fig. 4). Lying immediately on the dorsal side of the notochord is a cord of nervous matter which may be called the *cerebrospinal cord* and constitutes the central nervous system. Behind, this nervous cord tapers and ends in a point, or a small

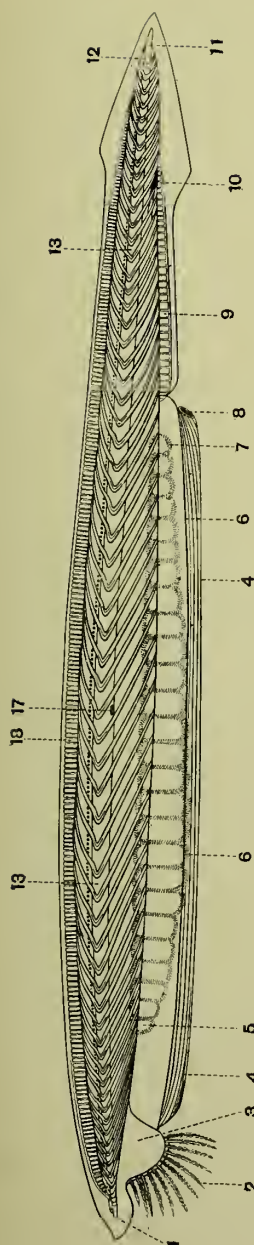


FIG. 4.—*Amphioxus lanceolatus* from the left "side" (after Lankester). The floor of the ventral groove is projecting and the atriopore is open. 1 anterior end of notochord; 2 oral tentacles; 3 oral hood (sides of buccal cavity); 4 ventral wall of atrium; 5 first gonad; 6 left metapleur; 7 last gonad (No. 26); 8 atriopore; 9 fin rays of anal fin; 10 anus; 11 hind end of notochord; 12 last myotome (62nd); 13 notochord; 14 position of opening of brown canal; 15 fin rays of dorsal fin; 16 fin rays of anal fin; 17 fin rays of dorsal fin.

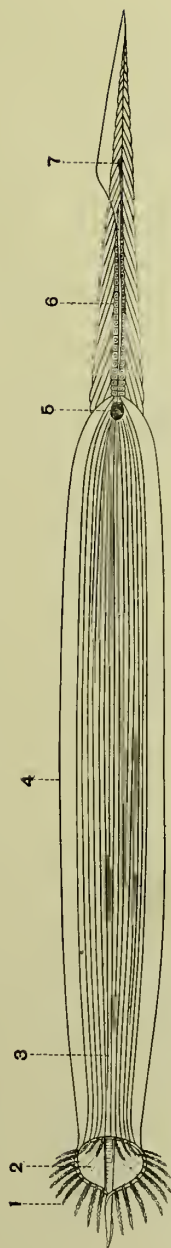


FIG. 5.—*Amphioxus lanceolatus*, ventral view (after Lankester). 1 oral cirri; 2 oral hood; 3 floor of atrium (plaited); 4 left metapleur; 5 atriopore; 6 fin rays of anal fin; 7 anus.

swelling, immediately over the hind end of the notochord ; in front it tapers very slightly, and possesses a somewhat blunt termination placed some little distance behind the front end of the notochord. On the ventral side of the notochord is the alimentary canal, which has the form of a straight tube extending between the mouth and the anus. The central nervous system therefore, lies entirely dorsal to and the alimentary canal entirely ventral to the notochord.

The alimentary canal consists of three parts :—

1. The **buccal cavity**. This is a short chamber opening to the exterior by the mouth and behind by a somewhat constricted opening into the pharynx.

2. The **pharynx** is the widest and longest portion of the alimentary canal, extending nearly half the length of the body. Its walls are perforated on each side by a number of obliquely directed slits (from above and in front ventralwards and backwards) which place its cavity in communication with a space lying immediately outside it, and called the *atrial* or *peripharyngeal* chamber. The atrial chamber entirely surrounds the pharynx except along the dorsal middle line (vide Fig. 10 and explanation). It opens to the exterior by the atrial pore—already mentioned—which is found at the hind end of the ventral groove (Fig. 5). The pharynx is mainly a respiratory organ, inasmuch as the blood which circulates in its walls and in the walls of the atrial cavity is aerated by the water which is continually being taken in by the mouth and driven by the action of cilia through the pharyngeal slits—or gill slits as they may be called—into the atrial cavity.

3. The **intestine** which extends as a straight tube from the hind end of the pharynx to the anus. The anterior part of the intestine is slightly dilated and receives ventrally a simple caecal sac, which, pushing the body wall before it, extends forwards in the atrial cavity on the right side of the pharynx and is called the *liver*.

#### Detailed Description of the Organs.

The **ectoderm** consists of a single layer of columnar or in some places cubical cells, which cover the whole external surface of the animal, are prolonged for a short distance into the buccal cavity and line the whole of the atrial cavity (Fig. 10). They



are without cilia except on the cirri, in the mouth and in the atrial cavity, and their outer surface is covered by a porous cuticle. Immediately beneath the ectoderm is a layer of fibrillated tissue called the cutis. Beneath this comes the subcutaneous tissue which consists of a gelatinous matrix containing sinuous fibres. The tissue within this has a similar form and extends between the myotomes, as the inter-muscular septa, to become continuous with the sheath of the notochord. In fact all the connective tissues of the body may be said to form a continuous framework which supports the organs and is on the whole of very similar structure throughout. In some parts it is firmer than in others and in some places it contains fibres, but it never presents a modification of a cartilaginous or osseous nature and never, except at the ventral ends of the primary pharyngeal bars, contains cells other than the epithelial cells which bound the spaces contained within it. These spaces are in some cases vascular and in others coelomic, but it is not possible in every case to be certain as to which of these two organs they belong. This absence of what we may call mesenchymatous elements from the connective and supporting tissues is one of the most remarkable peculiarities of *Amphioxus*.

As **skeletal** tissue we may rank the notochord, the supporting tissue of the buccal ring and the axial tissue of the buccal cirri, possibly also the axial tissue of the pharyngeal bars. The *notochord* is made up of a number of discs placed vertically, and transversely to the long axis, and consisting of gelatinous tissue. It is surrounded by a tough sheath of connective tissue, which is continuous with the rest of the connective tissue framework of the body. Nuclei are present on the dorsal and ventral sides in the neighbourhood of two spaces, the so-called dorsal and ventral lymph canals of the notochord.

The edges of the mouth contain a ring of skeletal tissue the buccal ring, resembling the notochord in structure. It consists of about twelve pieces on each side, and each piece gives attachment to a rod of the same substance, which occupies the axis and forms the support of one of the oral cirri.

The tissue of this buccal skeleton consists of a number of gelatinous discs surrounded by a fibrous sheath. By some observers it is claimed as cartilage, each disc being a cell and the surrounding membrane the

cartilaginous matrix. The tissue of the axial rods of the **pharyngeal** bars is sometimes described as skeletal. It consists of a clear chitin-like substance devoid of cellular structures except in the ventral bifurcated parts of the primary bars, which contain branched cells. Excluding the nuclei of the notochord, which is an endodermal structure, this is the only instance of a ~~mesodermal~~ tissue containing mesenchymatous elements.

The nerve-cord is surrounded by a tough sheath, which is continuous with the sheath of the notochord.

The **fin-rays** are found in the greater part of the dorsal fin in a single series, and in the anal fin in a double series (Figs. 4 and 5). They are absent from the cephalic fin, and from the anterior and posterior portions of the dorsal fin, and from the ventral part of the caudal fin. They consist of small cubical pieces of a tough fibrous connective tissue, which in the dorsal fin are continuous with the fibrous investment of the nerve-cord. They are more numerous than the metameres, there being four or five to each muscle segment.

The fins contain a longitudinal canal lined by epithelium and divided by septa into compartments. In the region of the fin-rays each of these compartments contains a fin-ray which pushes in its ventral wall and projects into it. The nature of these fin spaces is not known, but it is stated by Hatschek and others that they are, in the dorsal fin at least, coelomic in origin, being derived from the coelom of the muscle-plate (see below).

The **muscular system** consists of striated and unstriated muscular tissue. The striated muscles are composed of fibrillated rhombic plates, and are devoid of sarcolemma. They constitute the lateral muscles, the transverse muscles, the muscles of the lips and cirri, and the sphincter muscle of the velum and anus.

The great lateral muscle of the body is divided up into a number of successive segments, the **myotomes** (myomeres) by septa of connective tissue. These septa have a peculiar V-shaped course, and their insertion into the skin causes the V-shaped external markings already referred to (Fig. 4). The myotomes of opposite sides alternate with one another, i.e. the intermuscular septa of one side are opposite the middle of the myotomes of the other side. The full number of myotomes is laid down in the embryo. In *Amphioxus lanceolatus* there are about sixty-two on each side. The plate-like fibres of which these muscles are composed extend the whole length

of the myotome from septum to septum. The other striated muscles are very similar to the lateral muscle in structure, but the cross-striation is less marked, and they are not segmentally arranged, nor derived from the myotomes of the embryo. The transverse muscles extend from the ventral end of the lateral muscles to the middle line of the floor of the ventral groove, where they are inserted into a median connective tissue septum (Fig. 10). The unstriped muscle confers contractility on the walls of the intestine and larger blood-vessels. It is exceedingly inconspicuous and thin. It is doubtful indeed if it really exists as a distinct tissue.

The **nervous system.** The nerve-cord (cerebro - spinal cord) contains in its ventral portion a small circular central canal, which extends as a narrow fissure to the dorsal summit of the cord (Fig. 6). This canal is lined by columnar epithelial cells, some of which are continued into the substance of the cord as supporting fibres, while others may have the form of nerve cells. The cells lining the dorsal part of the canal are in close contact, so that the cavity here is virtual. The

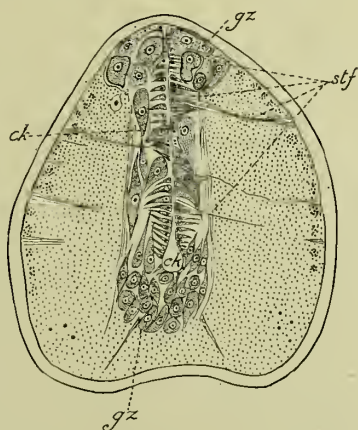


FIG. 6.—Transverse section of the spinal cord of *Amphioxus* (after Rohde). *gz* nerve cells; *stf* supporting fibres; *ck* central canal.

nerve cells are for the most part placed in the central part of the cord, and some of them are of giant size,\* and extend right across the fissure-like part of the central canal. On the ventral side of the canal, at short (metameric) intervals along the whole length of the cord behind the second myotome, are small groups of black pigmented cells.† These structures are probably sensitive to light. There is also a pigment spot, commonly called the eye, and placed at the front end of the cord in the anterior wall of the cerebral vesicle.

\* For the arrangement of these giant nerve-cells and of the giant fibres which issue from them, we refer the reader to Rohde, in *Zool. Beiträge*, 2, 1888, p. 169.

† Hesse, *Z. f. w. Z.*, 63, 1898, p. 456.

Anteriorly, though the cord itself tapers slightly, the central canal widens out into a spacious vesicle, the *cerebral vesicle*. This is the only representative of the brain of the Vertebrata. It gives off from its front dorsal wall a small hollow diverticulum, which ends blindly against the inner side of a small asymmetrical pit of ectoderm called the olfactory pit. This pit is placed on the left side of the body, is lined by ciliated cells, and is supposed to be olfactory in function. In the larva the process of the cerebral vesicle and the pit are in communication by a pore, which appears to be the persistent neuropore of the embryo. The cerebral vesicle is also said to possess a ventral diverticulum in the hinder part of its floor, which has been compared with the infundibulum of the vertebrate brain, but it is doubtful if it is always present. Posteriorly the cord tapers considerably and ends, usually in a small swelling, just short of the hind end of the notochord. In some cases it is said to extend as a filament round the hind end of the notochord on to the ventral surface.

The nerves issuing from this cord, except in the case of the first two, are dorsal and ventral in their origin and correspond with the dorsal and ventral roots of the spinal nerves of the Vertebrata. In *Amphioxus* they do not join and there are no ganglia on the dorsal roots. The dorsal nerves arise from the dorsal part of the cord. The nerves of the first two pairs (so-called cranial nerves) arise opposite one another, altogether in front of the myotomes. They are entirely sensory, and supply the preoral part of the body. Their finer branches possess nerve cells not far from their terminations. The remainder of the dorsal nerves alternate in their origin on the two sides, and contain motor as well as sensory fibres. They pass out behind the myotome to which they belong, and divide in the subcutaneous connective tissue into dorsal and ventral branches. The ventral of these supplies nerves to the transverse muscle of the sub-atrial floor. The dorsal nerves also supply the muscles of the lips and velum. The sides of the mouth (oral hood) and the cirri are supplied by the third to seventh dorsal nerves, and the nerves to the inner side of the lips of both sides are derived from the dorsal nerves which arise on the left side of the cord (reminiscence of larval condition, see below). The velar supply comes from dorsal nerves four to seven.

The ventral nerves (Fig. 7) are not united in bundles nor surrounded by a sheath, but issue as linear groups of fine fibres, which pass immediately to the adjacent myotome. They arise slightly anterior to the dorsal nerve of the segment to which they belong, and are exclusively motor for the muscles of the myotomes.

**Sense organs.** Scattered amongst the ectoderm cells are cells bearing short hairs. They are specially numerous at the front end of the body and round the mouth. They may be supposed to be tactile organs. They are also found in the mouth and on the velum. Organs which are supposed to be visual and olfactory have already been described.

The most striking peculiarities of the nervous system of *Amphioxus* as compared with that of the *Vertebrata* are the absence of an anterior cerebral enlargement; the peculiar form of the central canal, the dorsal fissure-like portion of which is probably represented by the dorsal fissure of the vertebrate spinal cord; the absence of a junction between the dorsal and ventral nerve roots and of a ganglion on the dorsal roots; and, lastly, the imperfect condition of the organs of special sense.

**The alimentary canal.** The mouth is a large, somewhat circular opening, placed on the ventral side of the body, a little distance from the front end. It leads into a spacious cavity, the buccal cavity, which is bounded by a fold of the integument called the oral hood (Fig. 4). The free edge of the oral hood, which may be called the lip, contains the skeletal framework already described, and bears a number (from twenty to thirty, increasing with age) of delicate ciliated processes, the oral cirri. The right side of this oral hood is, as has already been mentioned, continuous with the preoral ventral part of the median fin, which is in accordance with what might be expected

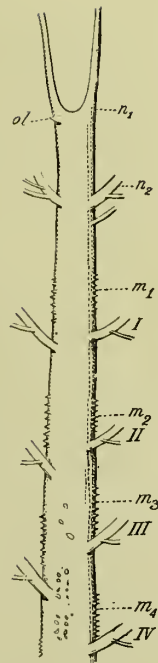


FIG. 7. —Anterior end of the nerve-cord of *Amphioxus* showing the nerve roots. The first two pairs,  $n_1$ ,  $n_2$ , have no ventral roots and arise opposite one another. On the right side one of the branches of the second nerve arises independently from the cord in the preparation from which this drawing was made (after Schneider). *ol* olfactory process;  $n_1$ ,  $n_2$  first and second nerves (cranial); *I*, *II*, *III*, *IV* dorsal roots of the next four pairs of nerves;  $m_1$ – $m_4$  ventral roots of the same.



from the development of the parts (see below). The buccal cavity is bounded behind, at the level of the anterior angle of the seventh myotome, by a muscular membrane, the *velum*, which separates it from the pharynx and is perforated by an aperture, which has been sometimes called the true mouth and is the actual opening which formed the mouth in the larva. The edges of the velum around this opening bear twelve delicate tentacles, the velar tentacles, which project backwards into the pharynx. The buccal cavity is lined by a ciliated epithelium, and bears on its roof slightly to the right of the median line a pit called Hatschek's pit, or simply the preoral pit (Figs. 8, 9). This organ is lined by a columnar epithelium, the cells of which bear stiff sensory hairs. It opens in a groove of columnar finely ciliated epithelium, which extends a short distance in front of it in the roof of the mouth and behind bifurcates into two ciliated grooves; these pass obliquely backwards and outwards to the velum, and then pass ventrally along the junction of the velum and sides of the mouth. They terminate either by simply coming to an end, or by running into one another on the floor of the buccal cavity. These two diverging

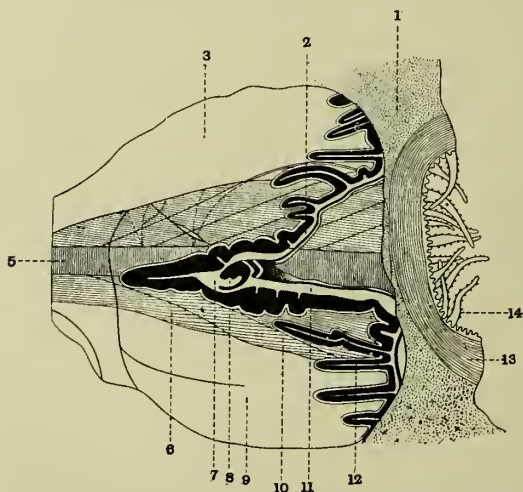


FIG. 8.—View of the roof of the buccal cavity of *Amphioxus lanceolatus* from below (after v. Wijhe). 1 posterior wall of buccal cavity; 2 ciliated groove of left side; 3 left side of preoral hood; 5 notochord; 6 second myotome; 7 Hatschek's (preoral) pit; 8 ciliated pit; 9 right side of preoral hood; 10 third myotome; 11 ciliated groove of right side; 12 accessory ciliated groove; 13 sphincter muscle of velum; 14 velar tentacles.

ciliated furrows give off accessory furrows, which are formed by folds of the antero-lateral walls of the main furrows. The accessory ciliated furrows pass forwards for a short distance on the roof and sides of the mouth. The whole structure constitutes the "wheel - organ" of J. Müller. It

is an organ for creating currents in the mouth back to the pharynx. The preoral pit which opens into its front part has been variously interpreted as a sensory organ and a gland.

If the preoral (Hatschek's) pit be regarded as a gland, it has been suggested by v. Wijhe that it is comparable to the neural gland of the *Tunicata*, and that the ciliated groove is comparable to the opening of that gland, the dorsal tubercle, the edges of which are frequently drawn out in a manner

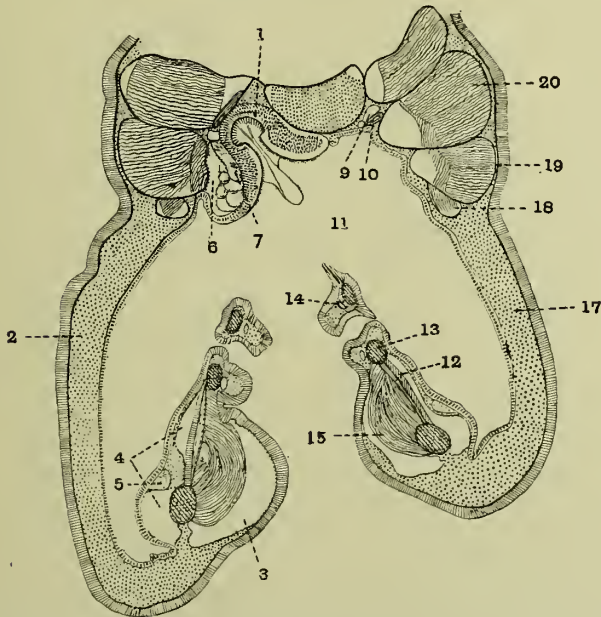


FIG. 9.—Transverse section through the middle of the buccal cavity of *Amphioxus lanceolatus* to show the preoral (Hatschek's) pit and the ciliated furrow (after v. Wijhe). 1 Hatschek's pit; 2 right side of preoral hood; 3 outer lip-cavity; 4 inner lip cavity (3 and 4 are parts of the left collar somite of the embryo); 5 labial nerve; 6 coelom (dorsal buccal, a portion of the collar somite of the embryo); 7 contorted blood vessel (continuation of right aorta); 9 aorta; 10 Hatschek's nephridium (a process from the pharynx); 11 buccal cavity; 12 internal labial muscle; 13 skeleton of cirrus; 14 cavity (lymph space) of cirrus; 15 external labial muscle; 17 left side of preoral hood; 18 second, 19 third, 20 fourth myotome.

very similar to the course of the ciliated groove of *Amphioxus*. Against this interpretation we must set the fact that the preoral pit, whatever its origin (see below), has no relation to the central nervous system. Moreover the interpretation of it as a gland is a very doubtful one. Van Wijhe describes a special part of the ciliated furrow just behind and in close connection with Hatschek's pit as the *ciliated pit* (Fig. 8, 8).

The pharynx is a large chamber tapering slightly posteriorly on account of the dorsal inclination of its ventral wall. Its side



walls are perforated throughout their whole dorso-ventral extent (except for a short distance behind the velum) by a number of vertically directed slits, which have a slight inclination ventralwards and backwards (more marked in the preserved than in the living animal), and which open into the atrial cavity. The dorsal and ventral parts of the pharyngeal wall are not perforated and constitute the hyperpharyngeal groove and the endostyle (hypopharyngeal groove) respectively. These terminate independently of one another posteriorly, but anteriorly they are connected by the peripharyngeal ciliated bands which arch round the pharynx immediately in front of the gill-slits. In front of the peripharyngeal bands there is a small portion of the pharynx adjacent to the velum without gill-slits.

The pharynx is lined by a ciliated epithelium, which is continuous through the slits with the ectodermal epithelium lining the atrial cavity. Along the endostyle there are four bands of specially glandular cells, which, like the remaining pharyngeal cells, bear cilia, and secrete the mucus, which passing forwards along the endostyle is driven upwards by the peripharyngeal bands into the front end of the hyperpharyngeal groove. Along this it is carried by ciliary action into the stomach. The food, consisting of small floating organic bodies brought into the pharynx by the ciliary currents, is entangled in this mucus and so separated from the water which passes through the gill-slits into the atrial cavity and out by the atrial pore.

New gill-slits continue to be formed long after the development has ceased, during the growth of the animal. They are consequently more numerous in large than in small specimens. In large specimens there may be as many as 180 secondary (see below) or 90 primary gill-slits on each side.

The new slits are formed at the hind end of the pharynx close to the junction with the stomach, as small circular perforations (see Fig. 24 in the account of the development). These soon become partly divided into two by the growth ventralwards of a process from the dorsal wall of the aperture (Fig. 25). This downward projection, from its resemblance to the tongue of a Jew's harp, is called the *tongue bar*. It eventually fuses with the ventral wall of the slit, so that the *primary* slit becomes completely divided into two *secondary* slits separated by the tongue bar. In correspondence with this we may call the parts of the pharynx-

geal wall intervening between two primary slits the *primary*

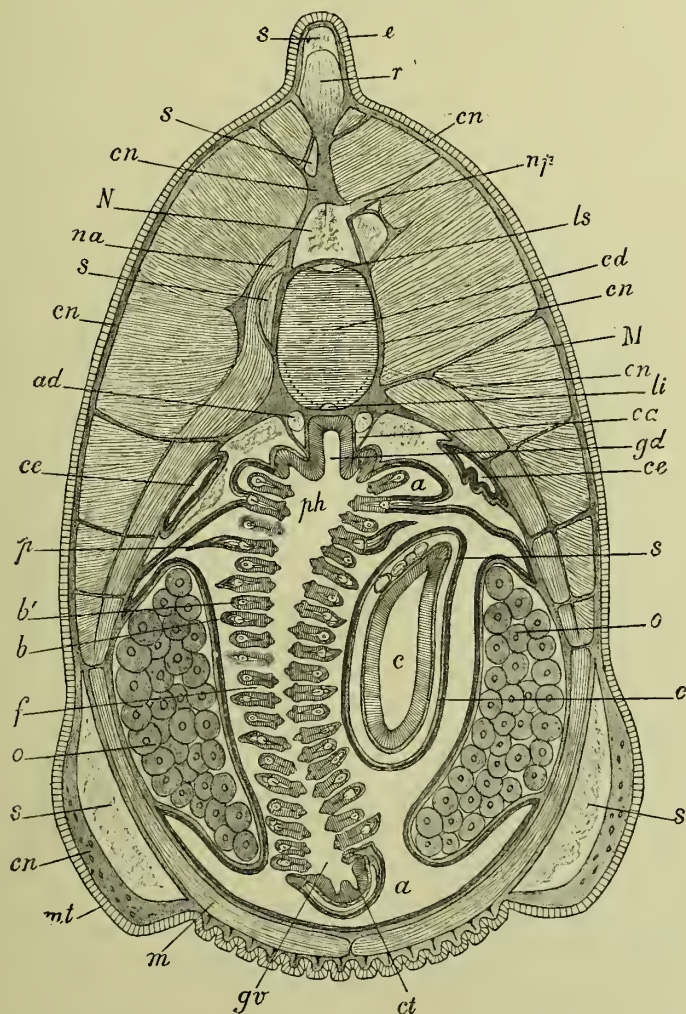


FIG. 10.—Diagram of a transverse section through *Amphioxus* in the hinder part of the pharyngeal region showing the brown canals (after Lankester, from Perrier). The division of the more ventral portion of the myotomes into two groups of fibres separated by a connective fascia is shown; *a* atrium; *ad* root of dorsal aorta; *b* primary bar; *b'* secondary bar; *c* liver (caecum); *ca* lymph space; *cd* notochord; *ce* tube of atriocoelomic funnel; *cn* connective tissue framework of the body; *e* *p* somatic wall covering caecum; *ct* skeletal plate of endostyle; *e* ectoderm; *f* branchial slit; *gd* hyperpharyngeal groove; *gv* endostyle; *li* ventral canal of notochord; *ls* dorsal canal of the notochord; *m* transverse muscle of atrial floor; *M* myotomes; *mt* metapleure; *N* spinal cord; *na* ventral, *np* dorsal root of a spinal nerve; *o* gonad; *p* portion of a fold in dorsal wall of atrium; *ph* pharynx; *r* dorsal fin ray; *s* so-called lymph-spaces. In the case of the hepatic caecum, *s* points to the blood-vessels.

*bar.* The primary gill-slits of opposite sides alternate with one another, as do the myotomes. In the adult they are more numerous than the myotomes, though when they first make their appearance, they correspond with them. The anterior primary slit on each side is not divided by a tongue bar.

On account of the obliquity of their direction a great many, both of primary and tongue bars, are cut in transverse section (Fig. 10). The primary bars differ from the tongue bars in structure (Fig. 11, *A, B*). In both there is an axial rod of a clear chitin-like substance (insoluble in potash), placed nearer the atrial than the pharyngeal side of the bar. In the primary bar this rod is double and without a cavity, while in the tongue bar it is single and has a cavity. These rods are continued inwards towards the pharynx as a thin membrane called the septal membrane (Fig. 11). The character of epithelium covering the bars may be gathered by an inspection of Fig. 11. On the outer side the ectoderm of the atrium is found. It is said to be non-ciliated and to be separated from the more extensive pharyngeal endoderm by some pigmented cells. The cilia of the endoderm vary in character on different portions of the bar, recalling the condition found in the Lamellibranch gill. The primary bar contains between the ectoderm and the skeletal rod a chamber which is a portion of the coelom, being continued dorsally into the dorso-pharyngeal coelom, and ventrally into the endostylar coelom. In addition three blood-vessels can be seen in the primary bar in the positions and with the names indicated in the figure. In the tongue-bar the visceral (10) and somatic (7) vessels are present, and in addition there is a space in the skeletal rod (3). This is interpreted by Lankester and Benham as coelomic, by others as vascular. According to Benham this space contains a blood-vessel (omitted in the figure) corresponding to the external blood-vessel of the primary bar (4). Successive primary bars are connected by transverse bars (*synapticula*), which thus pass across the primary slits, internally to the tongue bars, with which, however, they are connected (Fig. 12, *s*). The primary bars may thus be distinguished from the tongue bars in transverse section; and they may be distinguished by inspection of the pharynx as a whole for the skeletal rod of the primary bars bifurcates ventrally on reaching the level of the endostyle, whereas that of the tongue bars does not bifurcate. Dor-

sally the skeletal rods of both bars bifurcate and arch over the clefts to join the branches of the adjacent bars. Below the endostyle are some flat plates of skeletal tissue, which partially overlap one another. They correspond in number with the primary slits at the lower end of which they are placed.

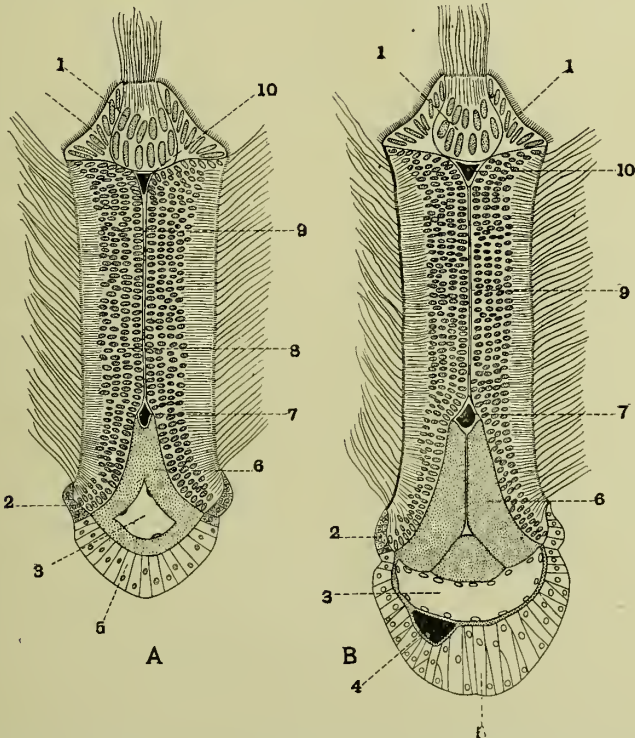


FIG. 11.—Transverse sections at right angles to the length of the pharyngeal bars of *Amphioxus lanceolatus*, A of a tongue bar, B of a primary bar (after Benham slightly altered). The relative sizes of the two bars is maintained. 1 endoderm epithelium on the pharyngeal end of a bar; 2 pigment cells; 3 coelom of the primary bar in B, coelom or external blood-vessel contained in the skeletal rod of the tongue bar in A (coelom according to Lankester and Benham); 4 external blood-vessel of the primary bar; 5 atrial epithelium; 6 skeletal rod; 7 somatic blood-vessel; 8, 9 septal membrane; 10 visceral blood-vessel.

The pharynx opens posteriorly into the intestine which runs straight back to open by the anus placed a little to the left of the median line at the level of the septum between the 51st and 52nd myotome. The anus is provided with a sphincter of striated muscular fibres. The intestine is lined by a columnar ciliated epithelium. The anterior part of the intestine is slightly dilated and called the stomach. It gives off a forwardly directed



diverticulum, the liver, which pushes before itself the ventral body wall, the whole projection lying in the atrial cavity alongside the pharynx on its right side (Fig. 10). This process is attached to the dorsal wall of the atrium in front. The lining cells of the hepatic caecum are coloured green in the living animal, as are the cells of the stomach from which it is given off. Outside the intestinal epithelium is a thin connective tissue layer which may contain unstriated muscular fibres.

**The atrial cavity** is a space lined by ectoderm and surrounding the pharynx and anterior part of the intestine ventrally and laterally. It opens to the exterior at the hind end of the ventral groove at the level of the 36th myotome. It extends back on the right side behind the atrial pore almost as far as the anus. Its lining cells are in part ciliated and pigmented with a brown pigment. The dorsal wall of the atrium is folded, in consequence of the fact that it is reflected on to each of the primary bars at a point considerably ventral to that at which it joins the secondary bars (Fig. 12, *ld*). This gives rise to somewhat puzzling features in transverse sections in which the dorsal regions of the primary bars appear to be connected to the side walls of the atrium by strands of tissue traversing the atrium (Fig. 10). The ligamentum denticulatum of J. Müller is this folded roof of the atrium cut longitudinally. It follows from this arrangement that the atrium is prolonged further dorsally in the region of the tongue bars than it is over the primary bars.

The *brown canals* are two tubes lined by a pigmented epithelium, and projecting into the dorso-pharyngeal coelom (Fig. 10). They lie parallel to the long axis of the body and probably end blindly in front at the 27th myotome. Posteriorly at the level of the junction of the pharynx and intestine they open by funnel-shaped apertures into the dorsal part of the atrial cavity, one on each side. They are to be regarded as forwardly directed diverticula of the atrium, of unknown function.

These structures are often called the atrio-coelomic funnels. They were discovered by Lankester. It is doubtful whether they end blindly in front or open into the dorso-pharyngeal coelom.

There is a well-developed **coelom** with which the gonads are in relation. A complete comprehension of the coelom cannot

be obtained until the development is studied, but the main features in its topographical arrangement seem fairly clear, and may be described at this point. In the adult there are many spaces in the tissues the exact nature and origin of which is not understood. Such will be referred to by the general term lymph spaces. It has been stated by some observers (Schneider, Lankester and others) that the coelom and vascular system are in certain parts of the body continuous. But having regard to the doubtful character of many of the body-spaces above referred to and to the difficulties to investigation presented by the vascular system, this statement cannot be accepted without further evidence.

In the region of the intestine there is a perivisceral cavity which is coelomic. It entirely surrounds the intestine except dorsally, where it is interrupted by the mesentery. In the region of the pharynx the same cavity is found, but it is broken up by the gill-slits into a number of parts all continuous with each other. There are two dorsolateral chambers, one on each side of the hyperpharyngeal groove. These extend a little way outward in the lateral walls of the atrium, and dip down into the folds of its roof along the primary bars. They constitute the *dorso-pharyngeal coelom*, and are continuous through the above-mentioned folds with the coelom present on the outer side of each primary bar. Ventrally the coelom of the primary bars opens into a median ventral chamber below the endostyle, called the endostylar coelom.

The arrangement of the coelom about the mouth, which has been described by v. Wijhe, is too complicated for description in this work: it is, however, referred to in the section on development.

**Excretory organs.** In the dorsal wall of the atrium lying between the atrial epithelium and the epithelium of the dorso-pharyngeal coelom are a number of tubes with a ciliated lining, which have been supposed to be renal in function (Figs. 12, 13). They correspond in number and position with the primary gill-slits and do not extend behind the region of the pharynx. They open into the atrium opposite the dorsal end of a tongue bar and at the summit of one of the dorsal pouches of the atrium found at that point (p. 26). They divide into two canals close to the opening; one of these passes forward and then turns round to travel for a short distance ventrally; the other passes backwards. They possess a variable number of branches (from 1-5), the number being least at the two ends of the series and greatest in the middle of it. Curious fibres ending in small knobs, each of which contains a nucleus, pass off from the ends of these branches and project into the coelom. These fibres are fine tubes ending blindly internally and opening into the secretory tube. They contain a long

vibratile flagellum, arising from the protoplasm around the nucleus at the internal knobbed end and extending along their whole length so as to project into the excretory tube (Fig. 13). They have been termed solenocytes from their resemblance to the fibres found on the excretory tubes of some invertebrates (e.g. polychaetous annelids). The tubes themselves are lined by a ciliated epithelium and a tuft of specially long cilia projects through the renal opening into the atrium. They receive a special vascular supply from the dorsal ends of the pharyngeal vessels, the blood being returned into the adjacent aorta. That these organs are excretory is inferred from their structure, which, as stated, closely resembles that of the excretory organs of some polychaetous annelids, etc., among the invertebrates, and on account of Weiss' experiments. He fed the

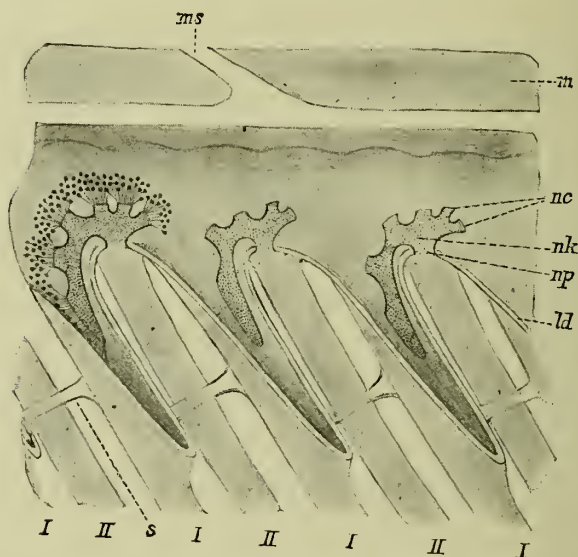


FIG. 12.—Dorsal portion of the left pharyngeal wall of *Amphioxus*, showing three renal canals, on one of which the solenocytes are shown; seen from the side, diagrammatic (from Korschelt and Heider after Boveri). *ld* optical section of the folded ventral wall of the dorso-pharyngeal coelom (ligamentum denticulatum); *ms* myotome; *ms* intermuscular septum; *nc* termination of the branches of the renal tube with the solenocytes removed; *nk* renal canal; *np* opening of the renal canal into the atrium; *s* synapticulum; I primary gill-bar; II tongue bar.

animal with finely-divided carmine, and then found that the cells of the main tubes contained carmine particles. But he also found carmine in the lining cells of the atrium including those of Müller's papillae. It is possible, of course, that Weiss' interpretation of these facts is correct, and that the carmine found in these cells was in the act of being excreted from the system into which it had been taken by the intestinal epithelium, but on the other hand it may well be that the carmine entered the cells concerned from the atrial cavity directly, in the same way that, according to Weiss' view it must have entered the intestinal walls.\*

\* Vide Weiss, *Q.J.M.S.*, 31, 1890, p. 497; and Boveri, *Zool. Jahrb.*, 5, 1892, p. 429. Goodrich, *Q.J.M.S.*, 45, 1902, p. 493.



**The vascular system.** There is no heart, but the larger vessels are peristaltically contractile. Lying on the ventral side of the endostyle in the pharyngeal wall there is a longitudinal sub-pharyngeal vessel, which corresponds to the heart and ventral aorta of the *Vertebrata*. Anteriorly it terminates by branching to the lips. Laterally all along its course it gives off branches, which have on their bases small contractile swellings called bulbils, to the primary bars. These ascend dorsalwards and open into the aortic root of their own side. The secondary bars receive their blood supply from the primary through the transverse bars. The roots of the aorta lie on each side of the hyperpharyngeal groove (Fig. 10). In the intestinal region they unite to form the single dorsal aorta, which gives off branches to the intestine and lateral body walls. Both the aortic roots are continued forward as the carotid arteries. These are joined together by a transverse anastomosis, and the right vessel gives off a large much convoluted branch which passes ventralwards at the level of the velum and ends blindly (Fig. 9). The anterior part of the right carotid has the form of a plexus, and gives off branches to the oral cirri of both sides.

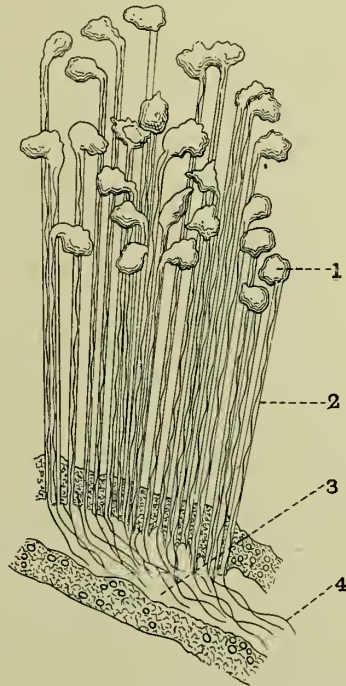


FIG. 13.—Portion of the excretory canal of a young *Amphioxus* with its solenocytes, from the living animal (after Goodrich). 1 solenocyte; 2 tube of solenocyte; 3 excretory canal; 4 flagellum of solenocyte.

The intestinal blood is collected into a sub-intestinal vein lying in the ventral wall of the intestine. This vein is not a simple vessel, but consists of a plexus of vessels, frequently communicating and lying side by side. Anteriorly the sub-intestinal vein appears to break up into a capillary system on the wall of the hepatic caecum. The blood of the caecum is collected into the

vein, the hepatic vein, which like the sub-intestinal vein consists of a plexus of vessels (Fig. 10). These commence in front and behind unite to form a single vein which is continued into the hind end of the sub-pharyngeal vessel. The hepatic vessels are said to communicate at the front end of the caecum with the dorsopharyngeal coelom, but this statement must be accepted with caution. There is undoubtedly a connection between the anterior end of the caecum and the lateral wall of the atrium. The blood is colourless; it contains amoeboid cells, and according to some observers a few red oval corpuscles.

In the larva the hind end of the subintestinal vein is continued directly into the sub-pharyngeal vessel. The direction of the flow of blood is forward in the subintestinal vein and subpharyngeal vessels, both of which are, according to J. Müller, contractile. It follows from this that the flow must be dorsalwards in the pharyngeal bars, backwards in the dorsal aorta and ventralwards in the peri-intestinal vessels. There is a considerable vascular development in the lateral walls of the atrium and a longitudinal vessel runs along the line of the gonads, but how these and the body-wall vessels generally are related to the main trunks described above is not known.

The other spaces of the body may be classed as lymph-spaces. They are lined by an epithelium and contain a coagulable fluid. Their origin and relations are not certainly known. Some of them, e.g. the lymph canals in the fins and certain spaces within the myotomes are said to be coelomic and derived from the mesoblastic somites of the embryo. Others may possibly be purely vascular; e.g. the large canal found in each metapleure—the metapleural lymph canals.

**Generative organs.** The sexes are separate. There are no external sexual differences. Generative ducts are absent, and the generative organs, which are segmented in correspondence with the myotomes and are placed in the lateral wall of the atrium at the ventral ends of the myotomes, delisce their products into the atrial cavity by rupture of their walls. From the atrium the generative products pass to the exterior usually through the atrial pore, but in some cases, according to the observations of Kowalevsky and Hatschek on the living, and of Marshall on the preserved animal, they occasionally pass from the atrium through the gill-slits into the pharynx and are spawned by the mouth. Spawning takes place at sundown only and fertilization is effected either in the sea or in the atrium.

In a fully-developed *Amphioxus lanceolatus* the gonads are somewhat cubical bodies, twenty-six in number on each side.

The first of them appears to be placed at the ventral end of myotome 10, and the last at the ventral end of myotome 35 just in front of the atriopore. They are contained in coelomic sacs, which in development are derived from the ventral ends of the myotomes, and to the wall of which they are attached.

The phylum possesses only a single genus\* *Amphioxus* Yarrell (*Branchiostoma* Costa). It is found in all seas. About ten species are known. They differ in the number of myotomes, the presence or absence of a caudal expansion of the median fin, the presence of gonadial sacs on one or on both sides of the body, the continuity of the right metapleur with the anal fin or the cessation of both right and left metapleur behind the atrial pore; the presence or absence of fin-rays and fin-ray spaces in the anal fin. There appears to be a considerable range of meristic variation in some of the species (Punnett). *A. lanceolatus* Pallas, Europe and most seas; *A. bassanum* Günther, right metapleur continuous with anal fin, gonads on right side only, anal fin with fin-rays and fin-ray spaces, Bass Straits; *A. cultellum* Peters, like the last, anal fin with chambers but without rays, Torres Straits; *A. lucayanum* Andrews, like the last, but without caudal fin, hind end of body being a urostyle-like process without myotomes, and fin-rays and chambers absent from anal fin, Bahamas.

It has been suggested that one or two species are pelagic, but this is uncertain.

**Development.** The development of *Amphioxus* presents some remarkable features, and contrary to our usual custom we have decided to give a full account of it in this work. Though strangely similar in many of its features to the type of development found in the Vertebrata, it presents some very marked features of difference. Of these we may at once mention the small size of the ovum, the archenteric origin of the coelom, the absence of any nephridial apparatus comparable to that of the Vertebrata, the origin of the gonads from the myocoel, and the extraordinary asymmetry of the larva.

Our account is based upon the important researches of Hatschek and Willy, who, as is well known, worked at the species found in the Pantano at Faro in Sicily.

The egg is small (.1 mm. in diameter), is surrounded by a vitelline membrane and contains but a small quantity of yolk, which is uniformly distributed. Only one polar body is attached to the ovum after deposition; it is probable that this is the second,

\* By some zoologists the phylum has been broken up into genera and sub-genera (Kirkaldy, *Q.J.M.S.*, 37, 1895, p. 303), but this, considering the small number of species and points of difference, seems hardly necessary at present.

the first having been formed in the ovary and rubbed off during the dehiscence. The segmentation is complete and almost equal, the segments of the lower pole being slightly larger than those of the upper. It leads to the formation of a hollow blasto-

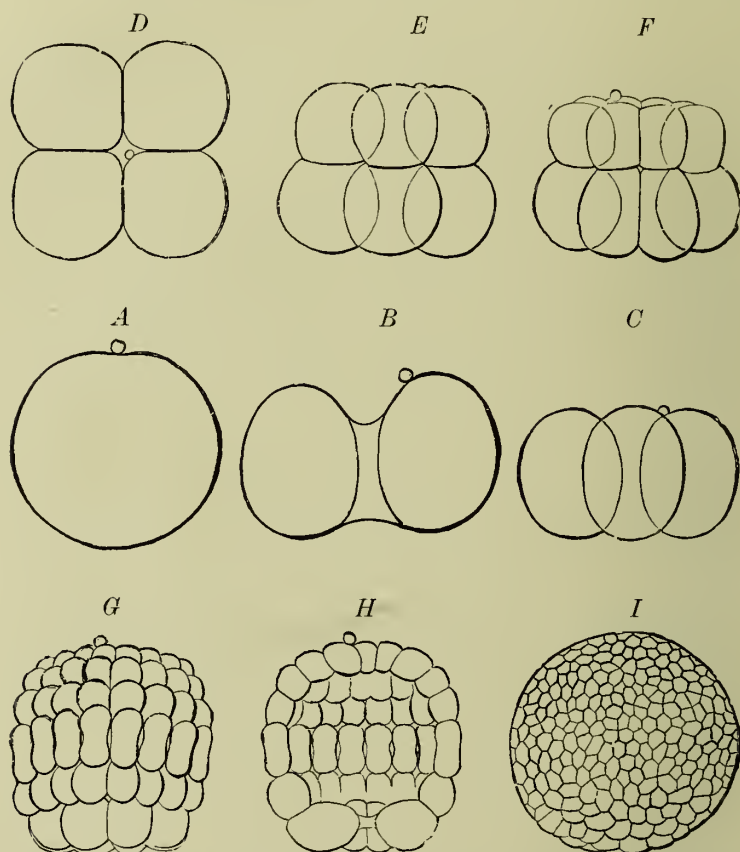


FIG. 14.—Cleavage of *Amphioxus* (after Salensky from Korschelt and Heider). *A* egg before cleavage, with polar body; *B* two-cell stage; *C* four-cell stage; *D* the same seen from the upper surface; *E* eight-cell stage; *F* sixteen-cell stage; *G* stage showing more rapid division at the animal pole; *H* the same in section; *I* surface view of blastosphere.

sphere (Fig. 14). This becomes invaginated to form a cup-shaped gastrula (Fig. 15). The blastopore, at first wide, soon narrows to a small opening placed at the hind end of the future dorsal surface. The embryo now elongates in the direction of the antero-posterior axis (Fig. 16), and the ectoderm of the dorsal

surface becomes more columnar to form the medullary plate (Fig. 17). As the medullary plate extends to the hind end of the dorsal surface, the blastopore is included in it. The lateral part of the ectoderm now becomes detached from the medullary plate, and grows over it (Fig. 17). This overgrowth begins at the hind end of the medullary plate, so that the blastopore is covered over and comes to open into the space between the overgrown ectoderm and the medullary plate (Fig. 18). Later the medullary plate curves over dorsally (Fig. 17), and by the junction of its two lateral edges forms the walls of the medullary canal (Fig. 26). From what has been said it is clear that the medullary canal, which is gradually developed from behind forwards, opens posteriorly into the archenteron by the blastopore and anteriorly to the exterior by the neuropore. As the medullary canal becomes the central canal of the nervous system, the blastopore is henceforward known as the neurenteric canal. It closes soon after the commencement of larval life. The anterior neuropore persists

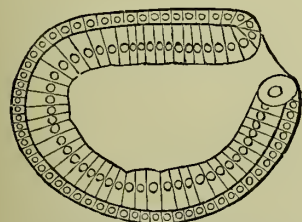


FIG. 16.—Gastrula of *Amphioxus* with narrow blastopore and flattened dorsal surface (after Hatschek from Korschelt and Heider).

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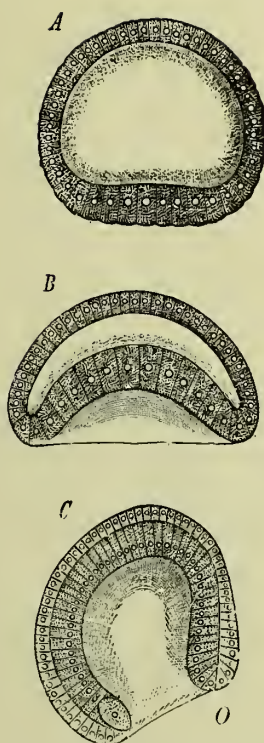


FIG. 15.—Formation of the gastrula of *Amphioxus* (from Claus, after Hatschek). *A* blastosphere; *B* commencing invagination of the lower surface of the blastosphere to form the endoderm; *C* later gastrula; all in optical section; *O* anterior lip of blastopore. The cilia of the ectoderm are omitted.

throughout larval life and only closes on the attainment of the adult state. It marks the site of the olfactory pit.

Meanwhile two pairs of dorso-lateral outgrowths of the archenteron are formed (Figs. 17, 18). The anterior of these retain their communication with the archenteron for some time and give rise

D



to the somites of the first pair. They are the "collar" somites of MacBride (Fig. 19, 6). The posterior outgrowths constitute the coelomic grooves of MacBride. They remain open to the gut for a considerable time behind, but as growth progresses they are continually constricting off sacs anteriorly (Fig. 19, 5). Eventually when about fourteen pairs of somites have been formed they become separate from the endoderm of the archenteron and form a solid plate on each side from which the remainder of the somites are successively developed. In addition to these two pairs of archenteric outgrowths there is a median anterior outgrowth (Fig. 19, 7). This grows back on each side

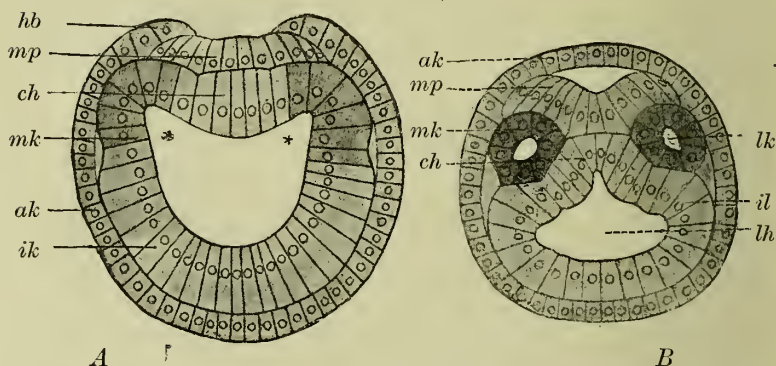


FIG. 17.—Transverse section through two embryos of *Amphioxus* to show the enclosure of the medullary plate and the formation of the coelomic pouches. A section through an embryo with the rudiment of one pouch and of the notochord. B section through a slightly older embryo, showing the complete separation of a coelomic pouch from the archenteron (from Korschelt and Heider after Hatschek); ak ectoderm; ch rudiment of notochord; hb lateral ectoderm growing over the medullary plate; ik, il endoderm; lh enteron; lk future coelom; mk coelomic pouch (future somite); mp medullary plate.

and becomes separated from the gut as a single cavity with two backwardly projecting horns. This unpaired anterior sac gives rise to the head cavities; it becomes divided into two, of which the right shifts ventrally, becomes thin-walled, and forms the cavity of the snout in the larva (Fig. 20). It becomes largely obliterated in the adult. The left head-cavity, on the other hand, becomes transversely placed beneath the notochord and opens to the exterior on the left side in front of the mouth (Fig. 20, w). It becomes the preoral (Hatschek's) pit, and gives rise by the extension of its lips to the wheel organ (p. 20). The collar-somites (so-called first pair) and the somites developed from the coelomic groove give rise to the mesoderm, body-cavity

and generative organs in a manner described below. The collar-somites send forward a process dorsal to the head cavities on each side, the walls of which give rise to the mesodermal structures of the preoral region.

While these changes have been taking place the notochord is developed. It arises as a groove of the dorso-median endoderm (Fig. 17 *B*), which is constricted off so as to form a solid rod of cells lying between the dorsal endoderm and the medullary plate. It develops from before backwards, except the front portion, which separates from the endoderm later than the rest and extends to the anterior end of the body.

The embryo becomes hatched and begins to swim freely in the sea by means of the cilia of the ectoderm cells at about the stage of Fig. 18, about twelve hours after fertilization. But it remains opaque and, being incapable of taking in food, is generally spoken of as an embryo until about the thirty-sixth hour, when the yolk is sufficiently absorbed to leave the tissues transparent, and the mouth, anus, and first gill-slit are formed (Fig. 20).

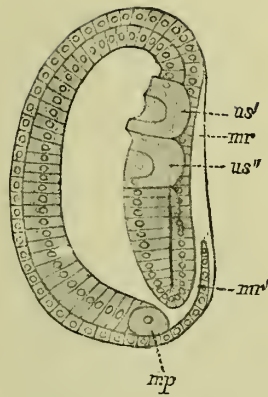


FIG. 18.—Longitudinal-vertical section through an embryo of *Amphioxus* with the rudiments of two somites (after Hatschek). *mp* pole-cells, the existence of which is now denied; *mr* uncovered part of medullary plate; *mr'* space between the medullary plate and overgrown ectoderm (future medullary canal); *us'*, *us'''* mesoblastic somites.

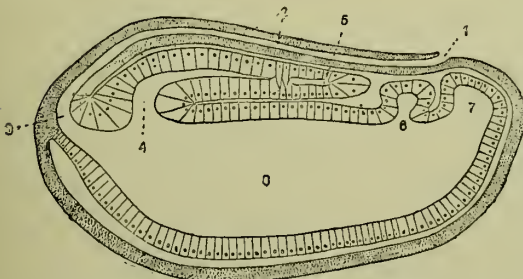


FIG. 19.—Diagrammatic longitudinal section through an embryo of *Amphioxus*, to show the formation of the coelomic sacs. The figure combines features which in reality would only be shown by two sections. 1 neuropore; 2 neural canal; 3 neurenteric canal; 4 coelomic groove; 5 somite constricted off from anterior end of coelomic groove; 6 cavity of first mesoblastic somite (so-called collar cavity); 7 head cavity; 8 archenteron.

The mouth is formed on the left side; the first gill-slit on the ventral middle line, soon moving on to the right side, and the anus at the hind end of the body slightly to the left of the middle line.

The larval



stage lasts for about three months, during which the larva swims freely usually at a considerable depth by the contraction of its body, and acquires the adult form and habits. The principal changes which take place relate to the formation of the gill-slits, of the preoral hood, and symmetrical adult mouth, and of the atrial cavity.

The mouth acquires a gigantic size and forms a most conspicuous object on the left side of the body (Figs. 21, 22). The gill-slits are formed successively on the ventral middle line to the number of fourteen.\* All of these except the last few shift soon after their formation on to the right side. They correspond in number to the myotomes in the part of the body

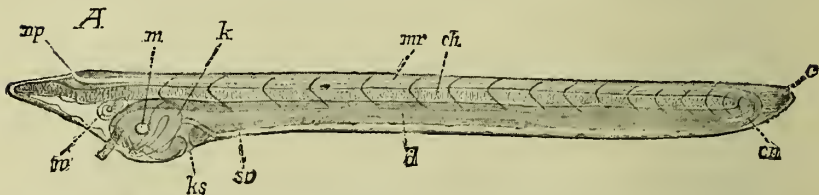


FIG. 20.—*Amphioxus* larva of about thirty-six hours from the left side, when the preoral pit-mouth, first gill-slit and anus are established (from Korschelt and Heider after Hatschek); *c* larval caudal fin; *ch* notochord; *cn* neurenteric canal; *d* alimentary canal; *h* right preoral sac; *k* club-shaped gland, which has acquired an opening to the exterior on the left side ventral to the mouth; *ks* first gill-slit; *m* mouth; *mr* nerve tube; *np* neuropore; *sv* sub-intestinal vein; *w* preoral pit (left head cavity).

in which they occur, but this relation is ultimately lost, when they become more closely packed and the myotomes increase in size. Of these fourteen first-formed gill-slits the first and the last five close up, so that eight only are left.

The atrial folds arise as ridges of the skin. Posteriorly they lie close together in the middle line enclosing between them a small groove (Fig. 23). Anteriorly they pass on to the right side, one on either side of the gill-clefts. By the union of these ridges, which begins in their posterior region and gradually extends forwards, the groove becomes converted into a canal,

\* These first formed gill-slits are often called the *primary* gill-slits, in contradistinction to the later formed secondary slits which, when the animal becomes symmetrical, are placed on the right side, the primary slits having passed over to the left side. Forster Cooper (*op. cit.*) describes a larva taken in the open ocean in the Maldivé Archipelago containing as many as thirty-one primary slits.

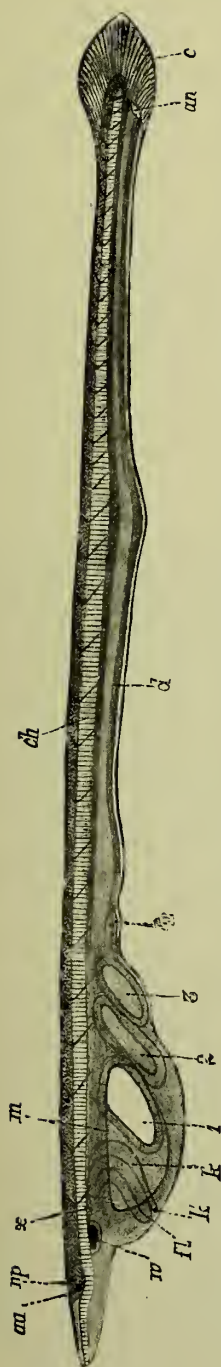


FIG. 21. — Larva of *Amphioxus* from the left side with three gill-clefts and thirty-six myotomes (after Lankaster and Willey from Korschelt and Heider). 1-3 first three gill-slits; 4 rudiment of the fourth; *an* anus; *au* eye spot; *c* larval caudal fin; *ch* notochord; *d* alimentary canal; *fl* rudiment of endostyle; *k* club-shaped gland; *k'* aperture of the same; *m* mouth; *n* p. mouth; *n* p. mouth; *n* p. mouth; *w* preoral pit; *x* Hatschek's nepritidium.

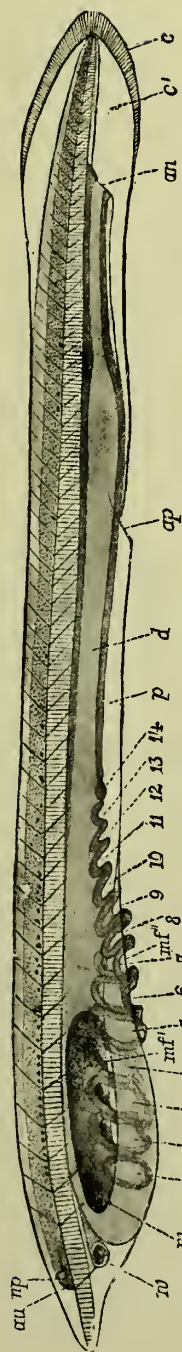


FIG. 22—Larva of *Amphibozus* with fourteen gill-slits and full number (61) of myotomes (after Lankester and Willey, from Korschelt and Heider). 1–14 first fourteen gill-slits; *an* anus; *ap* apertore; *au* eye spot; *c* larval caudal fin; *e* definitive caudal fin; *d* intestine; *m* month; *m'* edge of the right metapleural fold; *m''* edge of the left metapleural fold; *p* atrial cavity; *w* preoral pit.

the atrial cavity (Fig. 23). At their hind end they remain separate, thus giving rise to the atriopore. At first the atrial cavity is a small canal restricted to the ventral side of the pharynx. Later it becomes larger and acquires the adult relations.

Meanwhile a row of eight or nine gill-clefts appear on the right side of the body dorsal to those first formed (Figs. 24, 25). Both sets of gill-clefts acquire the U-shaped form, the tongue bar being developed (except in the first cleft (Fig. 25) which remains simple). The first-formed clefts then shift on to the left side of the body, and become the gill-clefts of the left side. At the same time the mouth shifts to the middle line, and the preoral

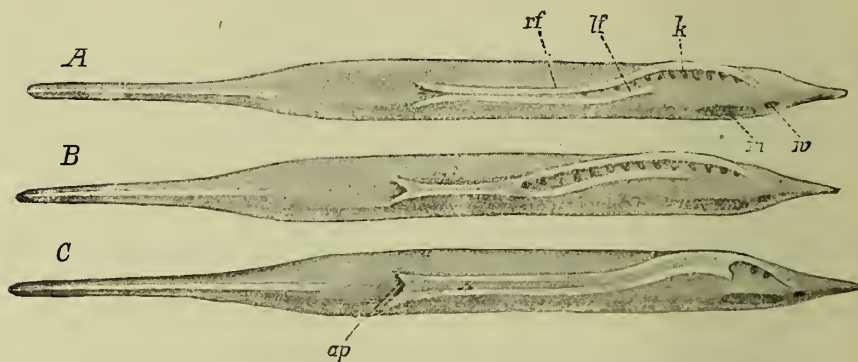


FIG. 23.—Ventral view of three larval stages of *Amphioxus* (after Lankester and Willey, from Korschelt and Heider); A, the atrium is still entirely open; B, the atrium is partially closed behind; C, the atrium is almost completely closed; ap atriopore; k gill-slits; lf left atrial fold; m mouth; rf right atrial fold; w preoral pit.

hood which had made its first appearance while the mouth was still on the left side becomes developed. The apertures of the club-shaped gland (see below) and of the ciliated pit are both enclosed by the preoral hood. The original mouth opening shifts to the back of the oral cavity and persists as the aperture in the velum.

The principal phases of the development are now accomplished and the larva, in the main symmetrical, assumes the sand-burrowing habits characteristic of the adult.

The mesoblastic somites, after their separation from the archenteron, which after that event is termed simply enteron, extend ventralwards on each side (Fig. 26), till they meet on the

ventral side of the alimentary canal. The septum between them (ventral mesentery) breaks down and the somites of the two sides become continuous.

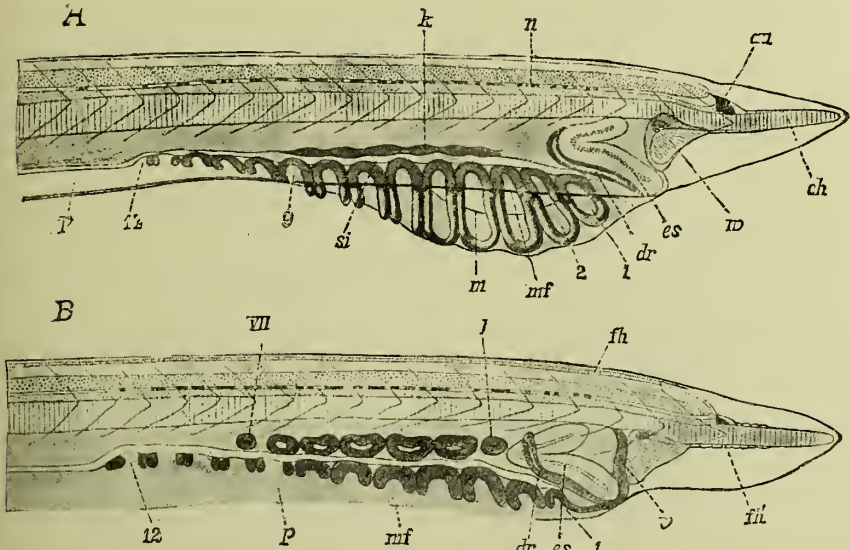


FIG. 24.—Two larval stages of *Amphioxus* from the right side, showing the origin of the gill-clefts of the right side of the adult (from Korschelt and Heider, after Willey). 1, 2, 9, 12, 14 first, etc., to fourteenth gill-cleft of future left side; I, VII first and seventh of the later formed set which eventually belong to the right side; *au* eye-spot; *ch* notochord; *dr* club-shaped gland; *es* rudiment of endostyle; *fh* dorsal, *fh'* ventral fin spaces; *k* rudiments of the later formed gill-clefts; *m* margin of mouth; *mf* edge of right metapleure; *n* nerve cord; *p* atrial cavity; *si* sub-pharyngeal vessel; *v* velum; *w* preoral pit.

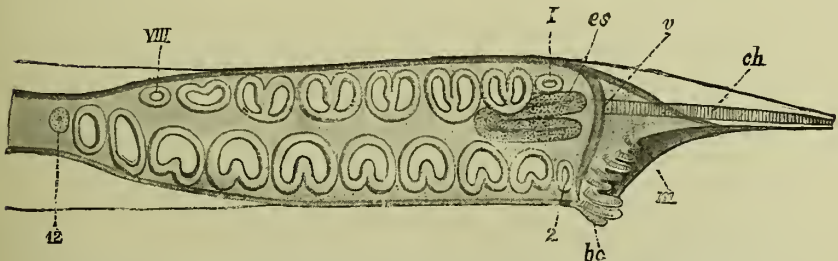


FIG. 25.—Ventral view of *Amphioxus* larva, rather later than Fig. 24 (from Korschelt and Heider, after Willey). 2 second, 12 vestige of twelfth cleft of the first-formed row, now passed on to the left side; I, VIII first and eighth of the later formed clefts of the right side; *bc* buccal cirri; *ch* notochord; *es* endostyle; *m* mouth (larval); *v* velum.

At the same time a septum is formed, dividing off the dorsal part of the somites from the ventral. The dorsal part becomes



the **myotome**; it retains its original segmentation and the septa separating the successive somites here persist as the myosepta (intermuscular septa). In the ventral portion (comparable to the lateral mesoblastic plate of the Vertebrata) the transverse septa, formed by the adjacent walls of the successive somites of the same side, break down and the cavities of the somite become continuous to form the splanchnocoel or body-cavity of the adult. The cells of the inner wall of the myotome become converted into muscles, and constitute the lateral muscles of the adult, while the outer wall which is applied to the ectoderm

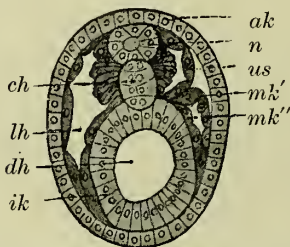


FIG. 26.—Transverse section through the middle of the body of an *Amphioxus* embryo with 11 somites. On the right side the section has managed to cut two somites (from Korschelt and Heider). *ak* ectoderm; *ch* notochord; *dh* enteron; *ik* endoderm; *lh* coelom; *mk'* somatic, *mk''* splanchnic layer of mesoderm; *n* nerve tube; *us* mesoblastic somite.

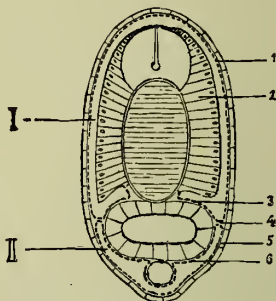


FIG. 27.—Transverse section of the middle of the body of an *Amphioxus* larva with five gill-slits, diagrammatic (from Korschelt and Heider). 1 outer wall of myotome (cutis layer); 2 inner or muscular wall of myotome; 3 commencement of the sclerotome; 4 septum between myocoel and splanchnocoel; 5 somatic mesoderm; 6 splanchnic mesoderm; *I* myocoel; *II* splanchnocoel. The sub-intestinal vein is shown in the splanchnic mesoderm.

remains thin (Fig. 27). The sclerotome is an outgrowth from the ventral and inner wall of the myocoel (Fig. 27). It acquires a considerable development extending dorsalwards between the muscles and the notochord and spinal chord (Fig. 28). Its inner wall gives rise to the sheath of the notochord and of the nerve cord, while its outer wall forms the so-called fascia-layer, or internal sheath (Fig. 29).

The dorsal part of the myocoel is said to give rise to the dorsal fin canal; and a ventral extension of the same space to the ventral fin canal. The myocoel appears to abort in the adult, but the sclerocoel probably in part persists as the lymph spaces on the internal sides of the lateral muscles.

In the region of the pharynx, the atrial cavity extends dorsally between the splanchnocoele and the ventral extension of the myocoele (Fig. 29), and the splanchnocoele becomes cut up by the gill-clefts into the sections of the coelom already described as occurring in the primary pharyngeal bars (p. 24). The dorsal and ventral regions of this part of the splanchnocoele furnish the dorso-pharyngeal (*sc*) and endostylar coelom (*ec*) respectively.

The first myotome is developed from the somites of the anterior pair, the so-called collar somites (p. 34), which retain their communication with the enteron longer than the others. This communication on the left side becomes elongated and gives rise to Hatschek's nephridium (Fig. 9, 10). These somites send back ventral extensions which lie in the developing atrial folds. It has been suggested that these give rise to the metapleural lymph canals, but this has been denied. The origin of the metapleural lymph canals is not certainly known.

Van Wijhe in his recent important paper (*op. cit.*) states that the walls of the collar cavity give rise to several myotomes. It is not quite clear to us whether this statement is based on embryological study or not. He further states that the second myotome of the body is the anterior of these myotomes which come from the collar-somite; thus implying that the walls of the head cavities (preoral somite) give rise to a myotome. So far as we know, the head cavities do not give rise to myotomes. The collar-coelom appears to give rise to the stomocoel and cavum epipterygium of van Wijhe, who states that the cavum epipterygium communicates with the metapleural canals. This confirms MacBride's statement that the metapleural lymph canals are parts of the collar coelom. The cavum epipterygium is also stated to communicate with the endostylar coelom through the coelom in the first branchial arch, which, being part of the splanchnocoele, it might reasonably be expected to do. The arrangement of the parts of the coelom about the mouth as explained by van Wijhe is complicated.

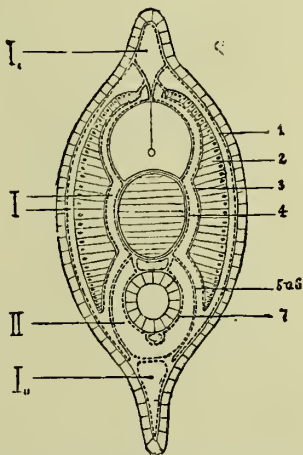


FIG. 28.—Transverse section through a young *Amphioxus* immediately after metamorphosis, between the atriopore and the anus, diagrammatic (from Korschelt and Heider, after Hatschek). 1 outer wall of myotome (cutis layer); 2 muscles; 3 fascia layer (outer wall of sclerotome); 4 skeletogenous (inner) wall of sclerotome; 5 u 6 ventral continuation of skeletogenous layer and somatic wall of splanchnocoele; 7 splanchnic ditto; *I* myocoele; *I'* dorsal *I'* ventral fin-space; *II* splanchnocoele.

The gonads are segmented in their origin. The generative cells are first seen as the thickenings of the coelomic epithelium at the ventral ends of the myotomes, on the anterior wall of the

myocoele. They soon come to project into the cavity of the somite in front, pushing the myosepta before them (Fig. 30).

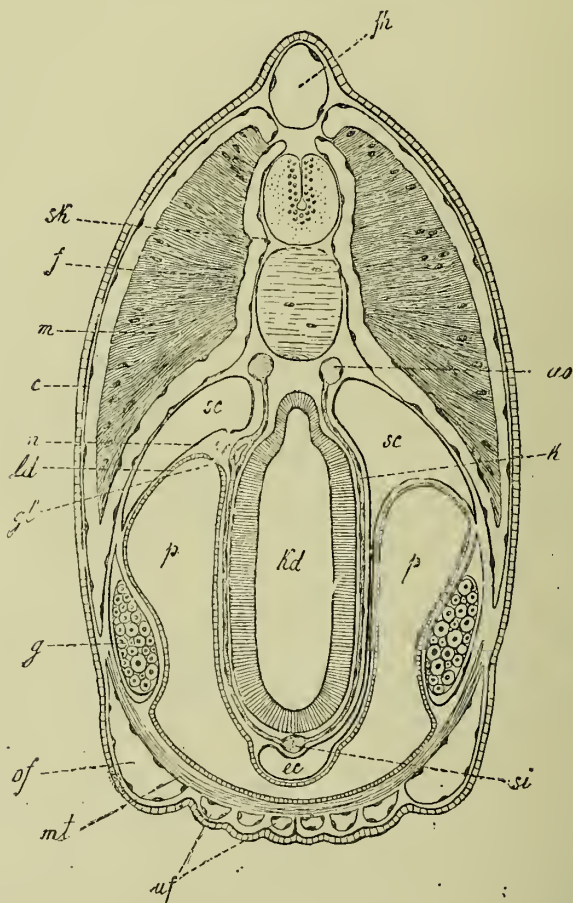


FIG. 29.—Transverse section through the branchial region of *Amphioxus* showing on the left the condition of a secondary, and on the right that of a primary gill-bar, diagrammatic (after Boveri and Hatschek, from Korschelt and Heider). *go* aorta; *c* cutis layer of myocoele; *ec* endostylar coelom; *f* fascia layer; *fh* dorsal fin canal; *g* genital sac; *gl* renal vessels; *k* vessel in primary bar; *kd* pharynx; *ld* ligamentum denticulatum; *m* muscle-plate; *n* renal canal; *of* metapleural lymph space; *p* atrial cavity; *sc* dorsopharyngeal coelom; *si* sub-pharyngeal vessel; *sk* skeletal layer of sclerotome; *uf* lymph canals of the atrial floor.

They lie therefore as small sacs in the preceding myocoele attached to its hind wall by a pedicle (Figs. 30 C, 31). Later, the part of the myotome in which they lie becomes separated from



the rest and forms the perigonadal coelom which lies in the outer wall of the atrium (Fig. 10).

The club-shaped gland and endostyle. The club-shaped gland

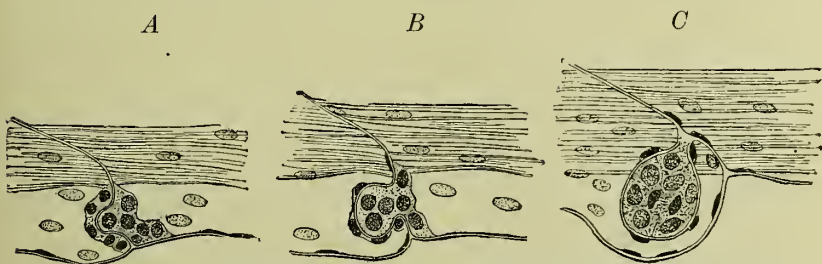


FIG. 30.—A, B, C.—Three side views of the ventral end of a myotome of a young *Amphioxus*, showing the development of the genital rudiment and its projection into the cavity of the preceding somite (from Korschelt and Heider, after Boveri).

is developed as a transverse groove on the floor of the pharynx and continued on to the right and left walls. It becomes constricted off from the pharynx, and acquires an opening to the exterior on the left side of the body just in front of the mouth. Later on the right end of it acquires an opening into the pharynx. The club-shaped gland is of unknown function and eventually atrophies. It has been suggested without any obvious justification that it is the metamorphosed anterior gill of the right side.

The endostyle is a ciliated tract of columnar epithelium just anterior to the club-shaped gland on the right side (Fig. 24). It subsequently becomes bent on itself in a V-shaped manner (Fig. 25), and grows backwards between the two rows of gill-slits. It is at first, therefore, on the right side of the body, but when the larva becomes symmetrical, it takes up its position in the ventral middle line.

From the above account it is clear that in the young larva

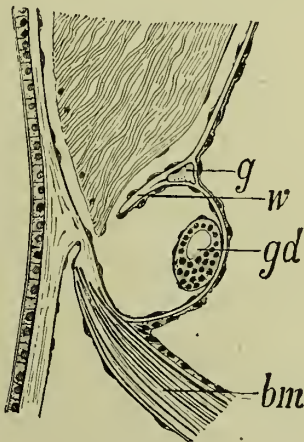


FIG. 31.—Transverse section through the genital rudiment of a young *Amphioxus* showing the separation of the perigonadal coelom from the myocoel. *bm* ventral muscle; *g* blood-vessel; *gd* gonad; *w* fold separating myocoel from perigonadal coelom.

the future ventral middle line of the pharyngeal region is on the right side of the body as shown by the first trace of the subpharyngeal vessel, the endostyle and the gill-slits ; whereas in the buccal region later median structures are on the left side. It results from this that, at the so-called metamorphosis when the larva becomes symmetrical, the buccal region of the body and the pharyngeal regions must rotate, so to speak, in opposite directions.

No satisfactory explanation of this extraordinary larval asymmetry has even been suggested. Though largely rectified in the adult a trace of it persists in the slightly asymmetrical position of the olfactory pit, the anus, and the continuity of the cephalic fin with the right side of the preoral hood, and in the innervation of the preoral hood (p. 18).

## CHAPTER III.

### PHYLUM VERTEBRATA\* (CRANIATA).

*Chordata in which the dorsal nerve cord extends some distance in front of the notochord, and is expanded at its anterior end into a brain. The axial skeleton is divided into an unsegmented cranial portion, which surrounds the brain, and a segmented vertebral portion which forms the axis of the body and protects the spinal cord.*

The various animals included in this phylum were first put together by Aristotle, who called them "animals with blood"; he also recognized the possession of a bony or cartilaginous skeletal axis as a common characteristic. But it was Lamarck who first adduced the presence of a vertebral column, as a most important character, and introduced before Cuvier the name of *Vertebrata* into the science. This term, however, is not entirely appropriate, for in some Pisces the sheath of the notochord is not segmented, and there are no vertebrae (Marsipobranchii, Dipnoi, some Ganoidei). Nevertheless, the term may fairly be retained, for not only has it the sanction of long usage, but the cases in which the vertebral column is not jointed are few in number and unimportant in character. As already pointed out, the segmentation of the vertebral column is corre-

\* Stannius, *Handbuch der Anatomie der Wirbelthiere*, 2nd ed., Berlin, 1854. Rathke, *Beiträge zur Bildungs und Entwicklungsgeschichte des Menschen und der Thiere*, Leipzig, 1833. Owen, *The Anatomy of Vertebrates*, 3 vols., London, 1866-68. Huxley, *A Manual of the Anatomy of Vertebrated Animals*, London, 1871. Gegenbaur, *Vergleichende Anatomie der Wirbelthiere*, Leipzig, 1898, 1901. Zittel, *Handbuch der Palaeontologie*, Munich, vols. iii., iv., 1887-93; and *Grundzüge der Palaeontologie*, Munich, 1895. (English translation, Macmillan and Co., 1900). A. S. Woodward, *Outlines of Vertebrate Palaeontology*, Cambridge, 1898. Balfour, *Comparative Embryology*, vol. ii., 1882. C. S. Minot, *Human Embryology*, New York, 1892.

lated with its rigidity, and is therefore best developed in those animals which have to support the body on land.

The **integument** consists of two distinct layers, the epidermis externally and the cutis internally. The epidermis is composed of many layers of cells, of which the upper and older layers are worn off, while the lower layer (*stratum malpighi*) is actively growing, and serves as a matrix for the continual renewal of the upper layers, and sometimes contains pigment. The cutis is principally formed of fibrous connective tissue, with which muscular elements—striped and unstriped—come into relation without however forming a dermo-muscular envelope, as in the Annelids. Some of the appendages of the skin are epidermal structures (hairs and feathers). Some are derived from ossifications of dermal papillae, which sometimes may even give rise to a hard and complete dermal armour (scales of fishes and reptiles, carapace of armadillos and tortoises). The epidermis is derived from the ectoderm of the embryo, the cutis or dermis being mainly a mesodermal product.

The endo-skeletal tissue of the lower Vertebrata and of all vertebrate embryos consists solely of cartilage (*Marsipobranchii*, *Elasmobranchii*), but in most groups osseous tissue, supplementing or, in the higher forms, largely replacing the cartilage, is present in the adult.

The **muscular tissue** may be divided into two categories : They are (1) the *somatic* or *myotome* muscles, which are derived from the epithelial wall of the myotomes or dorsal segmented parts of the mesoblast of the embryo, and (2) the mesenchymatous \* muscles, which are developed from the ventral part of the mesoblast (wall of the splanchnocoel). The myotome muscles are innervated exclusively by the ventral roots of the spinal nerves, and by the third, fourth and sixth cranial nerves, which are the only ventral nerve roots found in the brain. The mesenchymatous (visceral) muscles, which appear to be derived from mesenchymatous mesoderm, are innervated by the ventral roots in the trunk, but in the head by the fifth, seventh, ninth and tenth cranial nerves, which are usually regarded as dorsal nerve-roots, and which contain also afferent nerve fibres (see account of nerves under *Pisces*). The somatic muscles are cross-

\* Sometimes called visceral, but this is a bad name, as many of them lie in the body-wall.

striped and voluntary. The mesenchymatous muscles for the most part consist of unstriped fibres, but some of them are cross-striped, and even voluntary. The muscles of the heart and oesophagus are examples of cross-striped mesenchymatous muscles in the trunk ; they are not under the control of the will. In the head many of the mesenchymatous muscles are cross-striped and voluntary ; e.g. the facial muscles, the mandibular and the branchial muscles. The eye-muscles are myotome muscles, and supplied, as stated above, by ventral roots ; but they differ from the muscles of the great lateral sheet of myotome trunk muscles in the fact that their fibres are directed dorso-ventrally, and not longitudinally, as in the latter.

The dorsal nerve-cord extends in front of the notochord, and is enlarged in front to form the brain, which is constructed on the same fundamental plan in all classes. The posterior part constitutes the spinal cord. The skeletal investment of the brain is unsegmented, and constitutes the skull, while the spinal cord lies in a tube of the vertebral column, which always shows some sign of segmentation and is usually completely segmented. The spinal nerves, which are segmentally arranged, possess two roots, a dorsal and a ventral, which join. The dorsal of these roots carries a ganglion and contains afferent nerve fibres ; the ventral contains efferent fibres only. The brain possesses ten pairs of nerves, which are very similarly arranged in all Vertebrata. They differ from the spinal nerves in the fact that except in the case of three of them, they have the dorsal roots only. The third and sixth nerves may be regarded as the ventral roots of the fifth and seventh nerves respectively, and the fourth nerve must also be regarded as a ventral root, though it arises from the dorsal surface of the brain. The ninth and tenth nerves appear to be altogether without ventral roots. In the higher Vertebrata there are two additional pairs of cranial nerves, the eleventh and twelfth. Of the cranial nerves, the fifth, seventh, eighth, ninth and tenth are usually regarded, as being serially homologous with the posterior roots of spinal nerves, and are supposed to be related to a vanished segmentation of this part of the body.\* They resemble these in having

\* A short account of the modern views on the nature of cranial nerves and of nerves in general, and of cranial segmentation is given in the chapter on *Pisces*.



a ganglion, but, with the exception of the eighth, they differ from them in containing a fair proportion of efferent nerve fibres. The first and second cranial nerves, which supply the special sense organs of smell and sight respectively, appear to differ fundamentally from the other cranial nerves.

In all Vertebrata there are three organs of special sense on the head, the olfactory and visual, the innervation of which has just been referred to, and the auditory, which is supplied by the eighth cranial nerve. The connection of these organs with the head has profoundly modified the structure of both skull and brain.

A special visceral nervous system, known as the **sympathetic**, is nearly always present.

The alimentary canal presents very similar features throughout the series. It consists of a stomodaeum, pharynx, oesophagus, stomach, intestine. The stomodaeum contains the teeth and the openings of the salivary glands if present, and passes without any line of demarcation into the pharynx, which in all Vertebrata is at some time of life connected with the exterior by lateral apertures, the *pharyngeal apertures* or *visceral clefts*. These are never more (usually less) than eight in number on each side.\* In Fishes and Amphibia the first of these (spiracle) is always smaller than the others and may be completely absent; in the Amniota (Reptilia, Aves, and Mammalia) it is always present, and not smaller than the others. In Fishes and Amphibia the visceral clefts are used for respiratory purposes as in other *Chordata*, but they are never put to this use in the Amniota, where they appear to have no function at all. In such cases the respiratory organ of the adult is the lung, which is developed as a median outgrowth of the ventral wall of the pharynx. There are two other nearly constant features of the vertebrate alimentary canal, viz. (1) the connection of two large glands, the liver and pancreas, with the anterior part of the intestine, and (2) the connection of the generative and renal organs with the hind end of the intestine, which is commonly called the cloaca. The junction of the endoderm and ectoderm appears to take place at the anus, and there is practically no proctodaeum in the Vertebrata.

\* Except in some Marsipobranchs.



The **vascular system** is well developed, consists of arteries, capillaries and veins, and contains a red blood. There is a median ventral subpharyngeal vessel, the hinder end of which is especially muscular and contractile and differentiated as the **heart**. The **lymphatic system** consists of vein-like vessels containing a colourless fluid—the lymph—in which float numerous amoeboid cells (lymph corpuscles). These vessels commence by blindly-ending fine tubes or sinuses in the tissues, which gradually unite with one another to form the main lymph vessels, which open into the venous system. Special gland-like bodies, the so-called lymphatic glands, in which the lymph corpuscles are produced, are inserted in the course of the lymphatic vessels. The lymphatic system is a draining system, for the purpose of carrying away from the tissues the fluid which has exuded into them through the walls of the blood-capillaries, and is undoubtedly a specially differentiated part of the vascular system.

The **body-cavity** is a coelom, and has the usual relations of that organ to the urinary and reproductive organs. It is laid down early, making its appearance as a split (schizocoel) in the mesoblast; and in the Elasmobranchii, at any rate, a certain resemblance between it at its first appearance and that of *Amphioxus* can be detected (p. 33). But it differs from that of *Amphioxus* in that the ventral portions of the trunk somites are never distinct from one another, but form from the first a continuous splanchnocoel. In the adult the body-cavity is always divided more or less completely into a *pericardial* division in front and a *peritoneal* division or general body-cavity behind. In the mammals the latter is still further subdivided, in that two anterior horns are cut off from it to form the pleural cavities. There is no coelom in the head of adult vertebrata.

The **urinary organs** consist typically, in their origin at least, of segmentally arranged nephridia, which open internally into the body-cavity. Externally they open into a longitudinal duct which leads into the hind end of the intestine in almost all cases. Both nephridia and ducts develop as special portions of the coelom.

The **generative organs** develop from the lining of the unsegmented ventral part of the coelom (splanchnocoel), and

never present any trace of segmentation.\* In the female they retain this relation throughout life (except in Teleostei), but in the male the generative part of the coelomic epithelium always (except in Marsipobranchii) loses its relation with the general body-cavity in the adult.

The ovum varies considerably in character in the different classes. In Pisces (except Elasmobranchii) and in Amphibia it is comparatively small and holoblastic,† and the young are always hatched out in an immature condition as larvae. In Elasmobranchii, Reptilia, and Aves the ovum is large and meroblastic, and the young when hatched resemble the adult, a larval stage being absent. In Mammalia the egg is smaller than in any other Vertebrate, and except in one class undergoes almost the whole of its development in the oviduct, the young being born in a condition closely resembling the adult. An amnion, allantois and primitive streak are found in the embryos of all Reptiles, Birds and Mammals, but are absent from all Pisces and Amphibia.

The division of the Vertebrata into the four classes—*Pisces*, *Amphibia*, *Aves*, and *Mammalia* was first established by Linnaeus, though it had already been indicated in the system of Aristotle. The Pisces and Amphibia are cold-blooded animals (i.e. animals with a varying temperature); Aves and Mammalia are warm-blooded. Since Linnaeus' day, his group *Amphibia* has been split up into the naked Amphibia and into the scaly animals or *Reptilia*. Pisces and naked Amphibia have many characters in common, e.g. the branchial respiration, the frequent persistence of the notochord, the absence of an amnion and allantois, etc. On these grounds and in consideration of the many relations between Reptiles and Birds, Huxley has distinguished three principal groups of Vertebrata—the *Ichthyopsida* (Pisces and Amphibia), the *Sauropsida* (Reptilia and Aves), and the *Mammalia*.

\* See note on p. 88.

† In Teleostei the ovum though small is meroblastic.

## CHAPTER IV.

### CLASS PISCES.\*

*Aquatic vertebrata which breathe by means of pharyngeal gills and possess typically two pairs of appendages which never present any trace of a pentadactyle structure. Median fins supported, except in Marsipobranchs, by dermal fin-rays (dermotrichia) are always present. There are ten pairs of cranial nerves and paired posterior cardinal veins.*

Fishes are sharply marked off from all the other classes of Vertebrata by the form of their pectoral and pelvic appendages. These, which must be regarded as homologous with the limbs of the higher groups, are cutaneous expansions supported by skeletal structures, which, though presenting in their fan-like arrangement some distant resemblance to the skeletal structures of the pentadactyle limb, are yet never arranged on the penta-

\* Lacépède, *Histoire naturelle des Poissons*, 6 vols. Paris, 1798–1803. G. Cuvier et Valenciennes, *Histoire naturelle des Poissons*, 22 vols., Paris, 1828–1849. Baer, *Entwicklungsgeschichte der Fische*, Leipzig, 1835. J. Müller, *Vergleichende Anatomie der Myxinoiden*, Berlin, 1835–45. Id. Ueber den Bau u. die Grenzen der Ganoiden u. d. natürliche System der Fische, *Abh. d. Berlin, Akad.*, 1846. L. Agassiz, *Recherches sur les Poissons fossiles*, 5 vols. Neuchatel, 1833–44. Stannius, *op. cit.* Heckel and Kner, *Die Süßwasserfische von der österreichischen Monarchie*, Leipzig, 1858. A. Duméril, *Ichthyologie*, etc., 2 vols., Paris, 1866. Siebold, *Die Süßwasserfische von Mitteleuropa*, Leipzig, 1863. Blanchard, *Les Poissons des eaux douces de la France*, Paris, 1866. Cope, "Classification of Fishes," *Trans. Amer. Phil. Soc.*, 1870, and *Proc. Amer. Ass. for Adv. of Science*, 1871. A. Gunther, *Introduction to the Study of Fishes*, Edinburgh, 1880; and *Catalogue of Fishes in the British Museum*, vols. i–viii., 1859–1870. A. S. Woodward, *Catalogue of Fossil Fishes in the British Museum*, 3 vols. London, 1889–95. F. Day, *The Fishes of Great Britain and Ireland*, London, 1881–83. Jordan and Everman, *Fishes of North and Middle America*, *Bull. U. S. National Museum*, no. 47, Pts. 1–4, 1896–1900. T. W. Bridge, *Fishes in the Cambridge Natural History*, 1904. G. A. Boulenger, *Poissons du Bassin du Congo*, 1901.

dactyle plan. The ichthyopterygium, though clearly homologous with the cheiropterygium, is sharply marked off from it, and there are no intermediate forms connecting the two.

Though the structure of the limb skeleton, and possibly the possession throughout life of the paired posterior cardinal veins, are the only absolutely characteristic features of fishes, there is a number of features which, while not distinctive, are highly characteristic. We may enumerate some of these :—

1. Median unpaired folds of the integument, constituting the unpaired fins and supported by dermal structures called fin-rays or dermatrichia, would be absolutely characteristic were it not for the fact that the fin-rays are absent from the median fins of Marsipobranchii.

2. The absence of an internal opening of the nasal sac would be absolutely characteristic of the class were it not for the presence of internal narial openings in Dipnoi and of the pharyngo-nasal duct in Myxinoids.

3. Respiration by means of lateral pharyngeal apertures and gills is found in the adult in no other group excepting in a few genera of the Amphibia.

4. The absence of a cloacal bladder might perhaps be cited as a distinctive character, for it is present at least in the embryos in all the higher Vertebrata.

5. Excepting in the Dipnoi the auricle is undivided, and the ventral aorta is a tube of considerable extent.

6. Excepting in the Dipnoi there is nothing corresponding to the median inferior vena cava of the other classes.

7. The absence of a tympanic cavity and membrane, and of anything corresponding to the auditory ossicles of the higher types may, we think, be cited as a distinctive character, for these structures are very rarely, if ever, completely absent in the other classes.

8. The presence of the peculiar sense organ known as the lateral line might almost be regarded as a piscine character, were it not for the fact that it is not clearly present in all Marsipobranchii, and that it is found in some Amphibia.

9. The permanent division of the great lateral longitudinal muscles of the body into segments (myotomes) corresponding in number to the vertebral segments is only found outside Pisces in some Amphibia, and in the tail of some Repbelia.

The epidermis contains large mucous cells which discharge their contents on the surface. It may also contain pigment cells and leucocytes. In many fishes the slime which is excreted by the skin is poisonous.

The skin is seldom completely without skeletal structures (*Marsipobranchii*). As a rule **scales**, formed as ossifications of dermal papillae which are typically completely covered by the epidermis, are embedded in it. Fish scales \* are of three principal kinds: (1) Placoid scales which consist of small plates of bone in the dermis carrying an upstanding spine which projects freely, and is formed of dentine capped with enamel. These are found in Elasmobranchii and some Ganoids. (2)

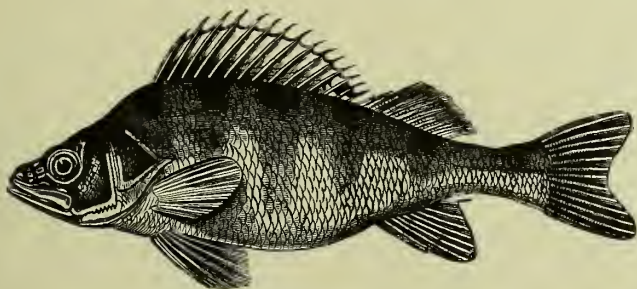


FIG. 32.—*Perca fluviatilis* (Régne animal).

Ganoid scales are bony plates covered with a smooth layer of a substance called ganoin. Ganoin † is a dermal product allied to vitro-dentine. These scales are entirely dermal, and if their surface is exposed, it is owing to the fact that the epidermis has been rubbed off. Such scales are found in most Ganoids. (3) Scales of varying thickness consisting of bone only, without ganoin. They are found in most Teleosteans, and are there called cycloid and ctenoid scales according to the nature of their edges.

The unpaired fins arise as a continuous fold of skin extending

\* A fuller account of the scales is given with the accounts of the orders. For principal recent literature, see Klaatsch, *Morph. Jahrb.* 16, p. 258, and 21, 1894, p. 153; F. Maurer *Die Epidermis u. ihre Abkömmlinge*, Leipzig, 1895. O. Hertwig, *Morph. Jahrb.*, ii. and vii. C. Röse, *Anat. Anz.*, 14, 1897; pp. 21 and 33. Nickerson, "The development of the scales of *Lepidosteus*," *Bull. Mus. Harvard*, 24, 1893.

† It was formerly supposed to be enamel and to be epidermal in origin, but this has been proved to be erroneous.



along the middle dorsal line of the trunk, and continued round the tail on to the ventral surface as far as the anus. It may persist in this form, but as a rule it becomes broken up into a variable number of dorsal fins, a caudal fin which consists of a dorsal and ventral part, and an anal fin between the ventro-caudal and the anus (Fig. 32). The unpaired fins are almost always supported by the so-called fin-rays or *dermotrichia*. These are horny fibres of the dermis (*Elasmobranchii*), or bony rods (*Teleostei*, Ganoids, *Dipnoi*) which may be segmented, and more or less soft and flexible (Malacopterygians) or stout and unsegmented (Acanthopterygians). These *dermotrichia* are absent only in *Marsipobranchii*. They are composed of two closely approximated halves, and are carried except in the case of the ventro-caudal fin, by the **somactids** or *radialia*. These are cartilaginous or bony rods, placed as a rule in the basal part of the fin-fold, and between the muscles of the back. They do not necessarily correspond in number with the vertebrae. They are usually segmented into two or three pieces, to the distal of which the *dermotrichia* are attached. The basal piece is sometimes called the *axonost*; in the *Teleostei* it is known as the interspinous bone, because it occurs between the spines (neural or haemal) of the vertebrae. The second piece is sometimes known as the *baseost*. In a few fishes (e.g. *Dipnoi*), the *somactids* articulate with the spines of the vertebrae.

The strong spine-like anterior fin-ray often found in *Teleostei* and bony Ganoids is formed of bone. In *Elasmobranchii*, the strong spines which are sometimes found in connection with the fins are tooth-like in structure.

The *dermotrichia* are of three kinds.\*

1. In *Elasmobranchii* and *Holocephali* they are unjointed, occasionally branched, fibrous rays of a horny consistency and without osseous tissue: these are called *ceratotrichia*. Similar *dermotrichia* are found in the larval fins and at the edges of the adult fins of *Teleostei* and Ganoids: in this case they are called *actinotrichia*. They are more numerous than the *somactids*.

2. In adult *Teleostei* and Ganoids the fins have jointed, branched, bony *dermotrichia* developed between the *actinotrichia* and the skin. They are supposed to be modified scales, which they sometimes resemble, and are called *lepidotrichia*. They correspond in number with the *somactids* except in the cartilaginous Ganoids, in which they are more numerous.

3. In the *Dipnoi* the *dermotrichia* have been called *kamptotrichia*

\* Goodrich, "Dermal fin-rays of Fishes," *Q. J. M. S.*, 1904.

They are branched, jointed bony rays, and appear to be merely modified *lepidotrichia*. They are more numerous than the somactids.

In all fishes the ventral part of the caudal differs from the other median fins in the fact that the dermatrichia (fin-rays) are supported directly by the haemal arches. These are frequently imperfectly segmented from one another, and may, in the adult, have the form of two or three bony plates, or even of a single plate. They are sometimes called, when ossified, the *hypural* bones.

A few Teleostei (eel-like forms, some Gadidae, etc.) and the Dipnoi constitute apparent exceptions to this rule as to the structure of the caudal fin, but in the former of these it is probable that the anal fin has fused with the ventral part of the caudal fin, for in a small portion of the ventro-caudal fin a few dermatrichia are carried directly by haemal arches. In the Dipnoi on the other hand, and in some Teleostei, the caudal fin appears to be entirely unrepresented, for the tail gradually tapers to its termination. What appears at first sight to be the ventro-caudal fin is really the anal fin, and in no part of it are the dermatrichia supported directly by the haemal arches. In the crossopterygian Ganoids, in which there is a diphycceral tail, the ventral dermatrichia of the caudal fin are clearly supported by haemal arches and not by somactids.

Considerable importance has been attached to the form of the tail and to the structure of the caudal fin in fishes. In the simplest cases the vertebral column is continued straight to its termination, and the dorsal and ventral part of the caudal fin are equal and symmetrical with each other. This type of caudal fin is called *diphycceral* or *protocercal*. In many fishes, however, the posterior part of the vertebral column is bent dorsalwards, and a special enlargement of the ventro-caudal fin is formed at a short distance from the end of the tail. This type of caudal fin is called *heterocercal* (Fig. 64), and is characteristic of Elasmobranchs and chondrosteian Ganoids. In such fishes the tail may be said to be bifid, presenting a dorsal lobe and a ventral lobe. The dorsal lobe consists of the real hind end of the tail with the dorso-caudal (if present at all) and part of the ventro-caudal fin, while the ventral lobe is the specially enlarged part of the ventro-caudal fin above described.

In *Teleostei*, and bony Ganoids, and some Selachians, the dorsal lobe thus defined shrinks and almost disappears relatively to the greatly enlarged ventral lobe, which now forms the whole of the tail fin, and becomes symmetrical in itself. Such a tail

is called *homocercal*. In many *Teleostei* the tail fin of the larva begins diphyccercal then becomes heterocercal and finally assumes the homocercal form. This correspondence between the developmental history of the tail and the three forms of tail fin found in living fishes is supposed to be highly significant from an evolutionary point of view, for it is supposed that the diphyccercal tail is the most primitive, and that the homocercal is the most specialised, the heterocercal tail intervening between the two. This supposition is to a certain extent borne out by palaeontology, which seems to show that Teleosteans are the most modern group of fishes. Unfortunately for the theory, however, the oldest fishes known to us had heterocercal tails and not diphyccercal, as the theory requires.

In addition to these three types of tail-fin, intermediate conditions have been named. For instance, the term *heterodiphyccercal* has been applied to slightly heterocercal tails in which the fin is much less developed on the dorsal side than on the ventral (some Crossopterygians, Fig. 104), while tails, in which the tail fin is externally symmetrical, but the hind end of the vertebral column is bent and extends some way into the dorsal lobe of the fin (*Amia*, etc.), are called *hemiheterocercal* (Figs. 107, 109). The true homocercal tail is distinguished from the hemiheterocercal by the fact that the vertebral column, which is bent dorsalwards, does not extend into the fin, but terminates in front of it.

As has already been mentioned, the dermatrichia of the ventro-caudal fin of all Pisces are attached directly to the haemal arches (for apparent exceptions to this see p. 55). In the homocercal tail of the Teleostean these haemal arches are called the *hypural* bones and are frequently fused together to form a single broad plate of bone. In Ganoids with heterocercal tails, when the upper lobe of the caudal fin (dorso-caudal) disappears it is replaced by a series of ridge scales: the "*fulcrum*" of palaeontologists: in Elasmobranchs, when absent, it leaves no trace.

The pectoral and pelvic fins also possess dermatrichia (fin-rays) and somactids (radialia). A certain number of the somactids are directly articulated to the limb girdles, and are then called *basalia*. There are usually three of these, which are then called pro- meso- and meta-pterygium, but their number varies considerably. The important point to notice is the arrangement of the peripheral somactids.\* In *Cladoselache*, a Palaeozoic fish, these are parallel to one another (Fig. 83), and the fin-skeleton may be termed *orthostichous*.† In most fishes, and notably in

\* Wiedersheim, *Das Gliedmassenskelet der Wirbelthiere*, Jena, 1892.

† The same feature is found in the pelvic fins of the Ganoid *Psephurus* (Regan, *Ann. and Mag. Nat. Hist.* (7), 13, 1904, p. 333.)

Elasmobranchs they are arranged in a fan-like manner, and the fin may be described as *rhypidostichous*. In Dipnoi the somactids of the fin are represented by a basal piece, followed by a row of them occupying the axis of the fin, with or without pre- and post-axial pieces placed like the barbs of a feather (Fig. 138). Such an arrangement may be termed *rachistichous* and *mesorachic*.

In some sharks and in the extinct *Pleuracanthidae* there is a succession of somactids forming a rachis, but the rachis is placed on one side of the fin and carries peripheral somactids mainly on that side.\* Such an arrangement may be called *rachistichous* and *pleurorachic* (Fig. 76).

A similar reduction in the number of basal somactids is sometimes found in the median fins of extinct fishes, e.g. in the anal fins of *Pleuranthus* (Fig. 87).

In the discussion of the vexed question of the origin of the vertebrate paired limbs, much attention is paid to the arrangement of these somactids (*radialia*). According to Gegenbaur the *Ceratodus* type (Fig. 138) of fin skeleton (*rachistichous*) is the most primitive, and this fin constitutes what he calls the *archipterygium*. On this view the skeleton of the paired fins and their girdles have originated from a branchial arch and its branchial rays; the girdle being derived from the branchial arch and the somactids from the branchial rays. One important objection (among others) to this view is that the branchial arches are in the gut-wall, whereas the limb girdles lie in the body wall.

On another and perhaps more acceptable view, if any view on these insoluble questions can be regarded as acceptable, the pectoral and pelvic fins are to be regarded as local specialisations of a once continuous lateral fold of the body wall, containing skeletal structures comparable to those of the unpaired fins, viz. basal segmented somactids (*radialia*) and peripheral dermo-trichia. This view was first suggested by Balfour. According to it the fin-skeleton of *Cladoselache* would be appealed to with its parallel somactids as being an obvious local specialisation of a once continuous fold, with parallel somactids all along its course.

It would be useless to study the **skeleton** except in detail,

\* There appears to be some dispute as to whether this side is pre- or post-axial. According to Wiedersheim and Fritsch, the side on which the majority of the rays are placed is post-axial, but according to the more generally received opinion it is pre-axial, the limb in the specimen from which Fig. 87 is taken having been displaced.

and for that we refer the reader to the account of the different sub-classes. We must content ourselves here with an account of its more general features, to which it is desirable to call attention.

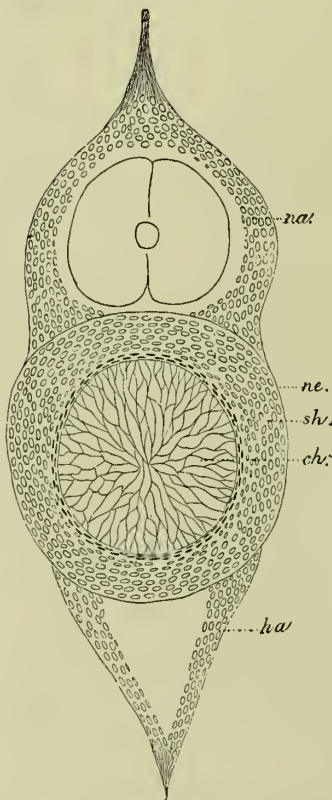


FIG. 33.—Transverse Section through the vertebral column of an advanced embryo of *Scyllium* in the caudal region; *na* skeletogenous tissue of neural arch, *ha* of haemal arch; *ch* notochord; *sh* notochordal sheath, which has acquired nuclei (*elastica interna*); *ne* outer chordal sheath (*elastica externa*) (After Balfour).

*externa*. Cells of the skeletogenous mesoblastic layer, which surrounds the notochord, appear now to penetrate the *elastica externa* and invade the *elastica interna* (Fig. 33), which thus becomes nucleated.

The chordal sheath sometimes remains as a continuous structure (Sturgeon, *Dipnoi*, etc.), but as a rule becomes seg-

The notochord forms the basis of the axial skeleton. It always persists in the adult, though it is generally considerably reduced. Its longitudinal extent is from the pituitary fossa of the skull in front to the end of the vertebral column behind. The notochord itself rarely forms an important element of the axial skeleton of the adult. Its supporting function—so conspicuous a feature in *Amphioxus*—is taken over by its sheath and by cartilaginous structures developed around its sheath. In the trunk these structures are, with few exceptions, segmented, and constitute the vertebral column; in the skull they are not segmented, and are known in the embryo as the parachordal cartilages.

At an early stage in the embryo a well defined structureless sheath is formed round the notochord. This is called the *membrana elastica interna*. A little later a second sheath is formed round this. This outer sheath, also structureless, is known as the *membrana elastica*



mented; in other words it becomes differentiated into alternately short fibrous and longer cartilaginous portions (Fig. 34). The fibrous portions become the intervertebral ligaments, the cartilaginous portions the bodies or centra of the vertebrae. The sheath thickens in the central part of the vertebral regions and constricts the notochord, so that the notochord assumes a beaded form, being narrowest in the middle of the vertebral regions and widest in the intervertebral (Fig. 34). In this way a bi-concave or amphicoelous centrum—a form eminently characteristic of fishes—arises.

When the centra are formed entirely or mainly from the chordal sheath they are called *chordo-centrous* (*Dipnoi*, *Elastomobranchii*). But it frequently happens that they are reinforced by cartilage derived from the arch-tissue. The arch-tissue arises from the mesoblastic tissue (skeletogenous layer), which surrounds the notochord, and is continued dorsally round the spinal cord. Four

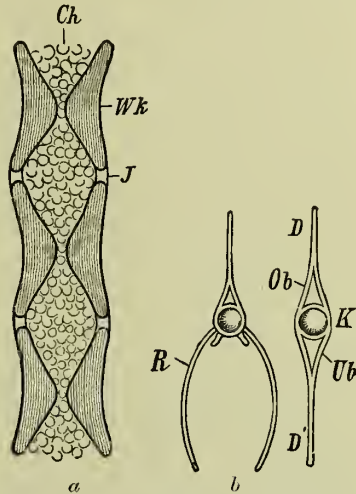


FIG. 34.—a Diagram of a longitudinal section of the vertebral column of a Teleostean with vertebral constriction of the notochord (from Claus). b vertebrae of a bony fish. *ch* notochord; *D* neural spine; *D'* haemal spine; *J* intervertebral ligament; *k* body of vertebra; *Ob* neural arch; *R* rib; *Wk* vertebral body.

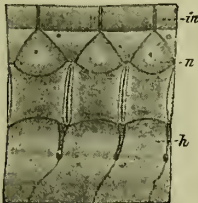


FIG. 35.—Three posterior trunk-vertebrae of *Centrophorus* (after Hasse from Gegenbaur). *n* neural arch with foramen for posterior root; *in* intercalated piece with foramen for anterior root; *h* haemal arch.

special concentrations of this tissue are formed adjoining the notochord, two dorsal and two ventral. In these the chondrifications which give rise to the neural and haemal arches begin. The neural arches do not always completely enclose the spinal canal, but are supplemented by the intercalated pieces (Fig. 35) which are placed between them, i.e. intervertebrally. The haemal arches may also be supplemented by intercalated pieces. These cartilaginous arches may spread out round the notochord outside

the membrana elastica externa and unite with each other, and so reinforce the vertebral centra. When the chordal sheath is inconspicuous, and the centra appear to be mainly derived from the arch tissue, the vertebral column is said to be *arcicentrous* (*Ganoidei*, *Teleostei*).\*

In this way a segmented vertebral column is established. In Teleosteans and bony Ganoids a further complication is added in the replacement of the cartilage by osseous tissue. The centra in the trunk (Fig. 34) carry as a rule short transverse processes, which may be called haemal arches, though they do not meet ventrally except in the caudal region, where they enclose a space containing the caudal artery and vein. The ribs are never more than short pieces of cartilage or bone attached to the outer ends of the transverse processes in the trunk region. There is no sternum in fishes.

The primitive cranium† consists of a cylinder of continuous cartilage, to which are attached anteriorly the nasal capsules widely open below, and posteriorly the auditory capsules. It is thus divided into four regions; the occipital surrounding the foramen magnum, the wide auditory region, the narrow sphenoidal or interorbital region, and the wide nasal or ethmoidal region. The junction of the parachordal with the trabecular region of the skull is marked externally by the foramen in the median floor, which transmits the internal carotid arteries (Fig. 36, 13), and internally by the posterior clinoid ridge which forms the hinder wall of the fossa for the lodgment of the pituitary body (Fig. 36, 6). In the embryo two elongated cartilages—the *parachordal* cartilages—are developed on each side of the cranial part of the notochord. They unite with each other around the notochord and form the *basilar plate* which gives rise to the occipital and part of the sphenoid regions. The auditory capsules which are developed round the membranous labyrinth become fused with this part of the skull. The anterior end of the skull in front of the pituitary fossa is formed by a second pair of embryonic cartilages, the *trabeculae*. To the front end of these the nasal capsules become attached, thus giving rise to the ethmoidal region.

\* Vide Gadow, *Phil. Trans.*, 186, 1895, p. 165.

† C. Gegenbaur, *Untersuchungen z. vergl. Anat. d. Wirbelthiere*, Heft 3. Leipzig, 1872. Id., "Ueb. d. Occipitalregion, etc. der Fische," *Kölliker's Festschrift*, Leipzig, 1887.

The hinder ends of the trabeculae embrace the front end of the notochord, so that the posterior clinoid ridge must be regarded as being formed by the hind end of the trabeculae. Moreover it must not be forgotten that the internal carotid artery enters the skull in the embryo through the space between the trabeculae before they fuse, so that the carotid canal also belongs to the hind end of the trabecular region.

Though the roof of the cranium is largely cartilaginous in fishes even when membrane bones are present on it, there is always a considerable fontanelle in which cartilage is absent. The cartilaginous cranium so constituted becomes in the Teleosts, Ganoids and Dipnoi replaced by bone to a varying extent, and reinforced by the development of osseous tissue in the adjacent connective tissue. The *membrane bones*, formed in the latter

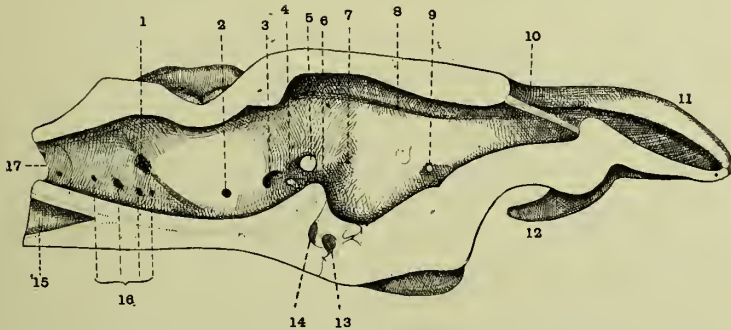


FIG. 36.—Median section of the cranium of *Hexanchus*, inner view (after Gegenbaur). 1 Foramen for vagus, 2 glossopharyngeal, 3 auditory, 4 facial, 5 trigeminal nerves; 6 posterior clinoid ridge; 7 foramen for oculomotor, 8 trochlear, 9 optic nerves; 10 fontanelle; 11 rostrum; 12 lateral process of ethmoid region; 13 foramen for carotid; 14 transverse canal in skull base; 15 notochord; 16 foramina for spino-occipital nerves; 17 neural arch of the first vertebra with nerve foramina.

manner, apply themselves to the subjacent cartilage and help in forming the cranial wall. The occipital region of the cranium is attached to the anterior end of the vertebral column, usually without any special articulation (except in *Batoidei* and *Chimaera*, etc.), the basioccipital region having the conical depression and form of a vertebral body. The cranial part of the notochord persists in the adult in some forms, but it more usually undergoes atrophy. It occasionally happens, as will be mentioned in the special accounts, that a few of the anterior vertebrae are fused with the occipital region of the cranium.

**Visceral Skeleton.**—The walls of the anterior part of the alimentary canal (mouth and pharynx) are supported and

strengthened by incomplete cartilaginous rings, analogous to the cartilaginous rings found in the trachea of the higher Vertebrata. Like the tracheal rings, they serve to keep open the tube—in this case the mouth and pharynx—through which the respiratory medium passes to the respiratory organ, but they differ from them in being divided up into segments which are movable upon one another by means of muscles. The **Visceral Arches**, as these structures are called, are placed in the splanchnic mesoderm, as shown by embryology, and therefore have nothing to do with ribs, with which they have sometimes erroneously been compared. They may be described as consisting of a series of cartilaginous rods on each side, joining one another ventrally, but usually (except in the case of the first two) ending freely dorsally without connection with other skeletal structures.

The first arch is called the **Mandibular**; its skeleton lies near the lips and constitutes the jaws. The second is called the **Hyoid Arch**: it lies in the pharynx wall between the spiracle and the first branchial cleft. The remainder, of which there are usually five, are the **Branchial Arches**: they lie in the pharynx wall between the branchial clefts, the last always occurring behind the last cleft. In *Heptanchus* there are seven branchial arches and seven clefts; in *Hexanchus* and *Chlamydoselachus* there are six.

The mandibular arch becomes closely associated with the cranium. It always becomes divided into two pieces: of these the dorsal piece forms the skeleton of the upper jaw and is called the palato-quadrato bar, while the ventral piece constitutes the cartilage of Meckel. The dorsal piece is longitudinally directed beneath the skull from the auditory to the ethmoidal region; it gives articulation at its posterior (quadrato) end to Meckel's cartilage. This upper segment of the mandibular arch presents two principal arrangements in fishes. In the one of these, that which is generally called the *hyostylic*, its hind end is not attached to the skull directly but is held up by the stout dorsal segment of the hyoid arch, which is for this reason called the hyo-mandibular. This is the arrangement found in most fishes. In *Chimaera* and *Dipnoi*, however, a different arrangement is found. In these and in some extinct fishes the palato-quadrato bar is fused with the skull not only posteriorly in the auditory region, but anteriorly in the ethmoid region and in the intermediate



sphenoid region. It is indeed fused all along with the side of the cranium and has the form of a laterally projecting triangular shelf, the projecting angle of which is the quadrate region and gives articulation to Meckel's cartilage. This arrangement is called **Autostylic** ;\* the hyoid arch taking no part in the suspension of the upper jaw.† It has been proposed to divide fishes into two great groups based upon the condition of the primitive upper jaw skeleton—the *Autostylici* and the *Hyostylici* ; but as we shall explain in the sequel, there appear to be good reasons for adopting a different arrangement.

In the *Teleostei*, *Ganoidei* and *Dipnoi* cartilage bones are developed in both the mandibular and hyoid arches to a varying extent and membrane bones may come to overlie them, largely supplementing them and even replacing them.

The **digestive organs** vary much in structure. The mouth, which is placed at, or near, the anterior end of the head, usually has the form of a transverse slit, and can sometimes be extended forward by means of the movable supporting bones of the upper and lower jaws. The buccal cavity is distinguished by its width, and by the great number of teeth it contains, which are developed from the papillae of the mucous membrane by dentinal ossification. There are often two curved parallel rows of teeth on the upper jaw ; an outer row on the premaxilla, and an inner row on the palatine, and there may also be a median unpaired row on the vomer. On the lower jaw there is only one curved row of teeth. There may also be teeth on the hyoid arch and on the maxillae, pterygoids, and parasphenoid, and, as a rule, on the branchial arches also, especially on the upper and lower pharyngeal bones. The teeth may be distinguished according to their shape into pointed conical prehensile teeth, and grinding teeth. They are developed in the mucous membrane and are attached to the skeletal structures by ligament or by ankylosis. In a few cases only are they implanted in sockets.

A small, hardly movable tongue is developed on the floor of the

\* The so-called *amphistylic* arrangement which is found in a few Elasmobranchs (see below) would seem to be a variety of the autostylic.

† The suspension of the mandibular arch, found in the skulls of Amphibia and Sauropsida, in which the palato-quadrate bar is not attached along its whole length, but only in the auditory and ethmoid region, must be regarded as a more typical form of the autostylic arrangement than that found in *Chimaera* and the *Dipnoi*.



buccal cavity, and the lateral walls of the pharynx are pierced by the gill-slits. Following the pharyngeal cavity, there is a usually short, funnel-shaped oesophagus, and a large stomach, which is frequently drawn out into a caecum of considerable size (Fig. 37).

Caecal appendages (pyloric appendages) are not unfrequently met with at the entrance of the lower mid-gut (small intestine) which is marked off by a valve; they probably serve the purpose of increasing the extent of the secreting surface of the alimentary canal. The intestine is usually several times coiled, and its internal surface is remarkable for the longitudinal folds of the mucous membrane; villi such as are found in the higher Vertebrates are only rarely present; but in the Selachians, Ganoids, and Dipnoi there is a peculiar spirally-coiled longitudinal fold—

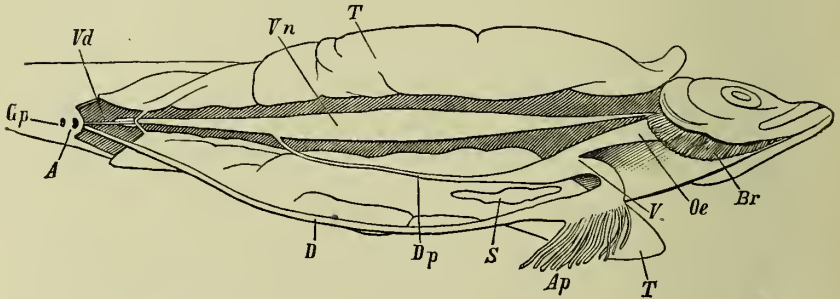


FIG. 37.—Alimentary canal and generative organs of *Clupea harengus* (after Brandt). *Gn* genital pore; *Ap* pyloric appendages; *Br* gills; *D* intestine; *Dp* pneumatic duct; *Gp* genital pore; *Oe* oesophagus; *S* spleen; *T* testis; *V* stomach; *Vd* vas deferens; *Vn* swimming bladder.

the so-called spiral valve—which contributes essentially to the enlargement of the absorbent surfaces. A rectum is not always clearly marked off, and when present is always short, and in the Selachians it is furnished with a caecal appendage. The anus is usually situated far back, and is always ventral, and in front of the urinary and generative openings, when the latter do not lead unto the rectum (cloaca). In fishes with jugular pelvic fins, and in some Teleosteans without pelvic fins, it is situated very far forward, and may even be on the throat.

Salivary glands are absent in fishes, but there is a large liver which is rich in fat and is usually provided with a gall-bladder; there is also usually a pancreas, which is by no means replaced in Teleosteans by the pyloric appendages as was formerly believed.

In many fishes the swimming bladder, an organ which by its mode of origin corresponds to the lungs, is developed as a diverticulum of the alimentary canal: it is sometimes closed, but sometimes remains in communication with the interior of the alimentary canal by the *pneumatic duct* (Physostomi) (Fig. 37, *Dp*). Its walls are formed of an external elastic membrane which is sometimes invested with muscles, and an internal mucous membrane. Glandular structures are sometimes present in the internal coat, and these may exert an influence on the enclosed air. The internal surface is usually smooth, but is sometimes provided with reticulated projections which lead to the origin of cellular cavities (some *Ganoidei*). Physiologically the swimming bladder is a hydrostatic apparatus, the function of which seems to consist essentially in rendering the specific weight of the fish variable. When it is present the fish must have the power of compressing it, partly by the muscles in its walls and partly by the muscles of the body, thus rendering the body specifically heavier so that it sinks. When the compression of the muscles is removed the compressed air will again expand, the specific gravity diminish and the fish will rise. If the anterior and posterior parts are separated and the pressure on them is unequal, then that half of the fish which is rendered specifically heavier will sink. Still more complicated relations, however, seem to exist.\*

**Respiration** is in all cases effected by gills, which may be supplemented by other structures, *e.g.* the lungs in the *Dipnoi*, and in *Teleostei* by vascular folds found in cavities (Fig. 38) in connection with the gill passages themselves or with the cavity beneath the operculum into which the gill-slits open. For a description of these we refer the reader to the special account of the *Teleostei*. The gills themselves are folds, containing many blood-vessels, of the mucous membrane of the passages which lead outward between the branchial arches to open on the side of the head. These passages, which may be short and slit-like, or long and tubular, open either directly to the exterior (*Elasmobranchii*) or their outer openings are covered by a fold of skin generally containing cartilaginous or bony supports and called the operculum. In this case they may be said to open into a branchial cavity which itself opens to the

\* See account of *Teleostei*.

exterior. The gills are either lamelliform (*Elasmobranchii*) and attached along their whole length to the interbranchial septa, or filiform and projecting (so-called pectinate gills of *Teleostei*, etc.). They are arranged in a row on each side of the branchial arch, so that each branchial arch carries two rows of gills (*holobranch*), one on its anterior and one on its posterior face. Sometimes there is only one row (*hemibranch*), and sometimes gills are absent on each side, or present only as a vestigial structure called a *pseudobranch*.

The general arrangement is as follows. The branchial passage between the mandibular and hyoid arches is called the *spiracle*. It is always reduced and is present only in most Elasmobranchs and some Ganoids. Behind this there follow typically five

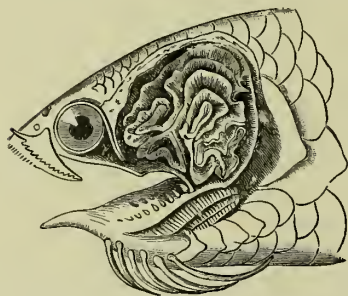


FIG. 38.—Head of *Anabas scandens* (Règne animal). The operculum has been removed to show the excavated superior pharyngeal bones (pharyngobranchials).

branchial passages or gill-clefts. The mandibular arch never carries more than a vestige of a gill, which is called the mandibular pseudobranch or pseudobranch of the spiracle. The hyoid arch never carries more than a demibranch and that on its posterior face. The first four branchial arches carry typically holobranchs, while the last branchial arch is always without a gill. It

thus happens that, if the hyoid arch carries a hemibranch on its hinder surface, the first four branchial passages have gills on both anterior and posterior walls, while the fifth branchial passage has a gill only on its anterior wall, the fifth branchial arch being always gill-less. In most fishes, however, the hyoid demibranch is reduced to a vestige, and is then known as the *hyoidean* or *opercular* (because the hyoid arch carries the operculum) pseudobranch. Externally projecting gills are found in the embryos of Elasmobranchs and a few Teleostei. They are not true external gills, but are much elongated internal gills. In the young *Polypterus* and some Dipnoi there appear to be true external gills.

The **brain** of fishes is small and does not fill the cranial cavity. It presents all the parts of the typical vertebrate brain.

It is perhaps chiefly characterised by the small development of the cerebral or prosencephalic part of the fore-brain. The anterior end of the medullary tube becomes at an early embryonic stage, when its walls are still epithelial, differentiated by two constrictions into three vesicles, the fore, mid, and hind cerebral vesicles. Of these the posterior vesicle or *hind-brain* gradually tapers behind into the spinal cord, and the portion of the medullary canal contained in it gives rise to the *fourth ventricle* of the adult. Its walls become transformed into the medulla oblongata, which is a development of the floor and sides of the hind-brain and is frequently called the *myelencephalon*. The *cerebellum* (*metencephalon*) is a special development of the anterior part of the dorsal wall of the hind-brain. The greater part of the dorsal wall remains throughout life at the epithelial stage and never develops nervous tissue. The mesoblast (*pia mater*) overlying this permanently epithelial wall becomes especially vascular and gives rise to the choroid plexus of the fourth ventricle.

The middle vesicle or mid-brain (*mesencephalon*) gives rise by its roof and sides to the *optic lobes* or *corpora bigemina*, and by its floor to a stout nervous mass consisting largely of strong bundles of nerve fibres which in the mammalian brain constitute the *crura cerebri* or peduncles of the cerebrum. The portion of the medullary canal in the mid-brain is the *iter a tertio ad quartum ventriculum* or *aqueductus sylvii*.

The anterior vesicle or fore-brain becomes early differentiated into three parts; a posterior part, the *thalamencephalon*, the central canal of which constitutes the *third ventricle*; a ventral part usually described as part of the thalamencephalon, the *infundibulum*; and an anterior part the *prosencephalon* or *cerebrum*, the ventricle of which is the *second ventricle*. The cerebrum is usually divided into a right and left lobe by a longitudinal vertical constriction, but this happens rarely (*Dipnoi*, *Marsipobranchii*) in fishes, though there are sometimes indications of this division in the form of a longitudinal surface groove, and in *Elasmobranchs* the contained ventricle is actually divided into a right and left ventricle which open behind into the third ventricle by the *foramen of Munro* and are termed the *lateral ventricles*.

The anterior end of the cerebrum is always marked off as two lobes of varying size and shape into which the second ventricle



is continued (as the *first ventricle*) and which give off from their anterior ends the olfactory nerve fibres: they are called the *olfactory lobes* or the *rhinencephala*. In the embryonic brain before the differentiation into thalamencephalon and prosencephalon has been effected, the fore-brain becomes bent ventrally, forming an angle with the posterior part of the basi-cerebral axis. This bend in the cerebral axis constitutes the cranial flexure; it takes place, roughly speaking, at the junction of the fore-brain and mid-brain and a short distance behind the front end of the notochord, the anterior end of which is under the posterior part of the fore-brain. The notochord is therefore involved in the cranial flexure and its front end becomes hook-shaped. The other organs of the anterior end of the head are also affected as is shown by the somewhat longitudinal disposition of the anterior gill-slits and arches (Fig. 39) as compared with the transverse disposition of those behind. In consequence of this bend in the nerve axis the anterior end of the neural tube becomes eventually directed ventralwards and, by a posterior outgrowth, backwards beneath the floor of the mid-brain: it constitutes the *infundibulum*, which has already been mentioned as one of the three divisions into which the fore-brain is differentiated. In addition to the infundibulum, a fourth division of the fore-brain has to be distinguished. At an early embryonic stage, before the prosencephalon is marked off, the anterior cerebral vesicle gives off a right and left lateral outgrowth: these are the *optic vesicles*. They at once become applied externally to the lateral skin of the head, and their connection with the brain becomes constricted to form a stalk-like structure which eventually becomes solid and forms the optic nerve. At the same time the cavity of the optic vesicle becomes obliterated by the invagination of its outer wall next the skin upon the inner wall on the brain side. This collapse of the optic vesicle, if not caused by, takes place in connection with the formation of the lens from the outer ectoderm at the point where the optic vesicle before its collapse touched the skin; it gives rise to the formation of a two-walled optic cup, the mouth of which is occupied by the lens and the double wall of which becomes the *retina* of the eye.

To return to the fore-brain. When the cranial flexure is established, the posterior part of its dorsal wall looks forward.



This part becomes greatly developed and produced forwards into a large vesicle, the front part of which soon becomes marked off as the rudiment of the cerebrum or prosencephalon. This forward growth is shown by the subsequent relations of the optic nerve to have taken place behind (in the original position of the parts) the attachment of that structure (*optic chiasma*) to the cerebral roof (Fig. 113). If this interpretation of the complex embryonic growths is correct, it would appear that the cerebrum is derived from a dorsal extension of the original fore-brain just behind the point of origin of the optic nerves, and that the olfactory nerves which are developed from the front end of the cerebrum and are usually described as the first pair of cranial nerves, are in reality the second, the optic nerves being anterior to them in position. The optic nerves then are attached to the roof of the original fore-brain at about halfway between its front and hind ends. A ganglionic mass is formed on each side at this point in the side walls of the fore-brain; these great ganglia are the *optic thalami* and lie in the adult brain at the side of the third ventricle, constituting the chief bulk of the thalamencephalon. Immediately in front of the optic thalami two great ganglionic developments are formed in the ventral wall of the cerebral outgrowth: these are the *corpora striata* found in the adult on the floor of the second ventricle or, if it is divided, of the lateral ventricles.

The front end of the cerebral outgrowth also gives rise to nervous tissue of the olfactory lobes.

We now come to the roof of the reconstituted fore-brain, after the cerebral outgrowth has been formed.\* This roof is divided into two parts by the velum transversum (see below). Of these the posterior part, the part overlying the third ventricle, remains in all Vertebrates almost entirely in an epithelial condition. It gives rise by its posterior part to the *epiphysis* or *pineal body*. To this we shall return shortly. The anterior part, the part belonging to the cerebral rudiment, is called the *pallium*. It is marked off from the posterior part by a transversely directed fold of the epithelial roof. This fold dips down into the ventricle at the junction of the thalamencephalon and prosencephalon and encloses between its two laminae a vascular development of the pia mater, which is always present and gives rise in the

\* Minot, *American Journal of Anatomy*, 1, 1901, p. 81.

higher brains to the choroid plexuses of the lateral ventricles. It is called the *velum transversum*.

This folded-in part of the roof is generally regarded as belonging to the cerebrum: in all Vertebrata it retains throughout life its epithelial condition. In front of it, the roof of the brain (pallium) behaves in a different way in different animals. In Elasmobranchs, Marsipobranchs, Dipnoi, and in all Vertebrata above fishes, it loses its simple epithelial condition and develops nervous tissue, forming the dorso-lateral part of the cerebral hemispheres above the lateral ventricles. In most other fishes, Teleosteans, and Ganoids, the pallium retains its epithelial condition throughout life, so that in these groups the roof of the lateral ventricle remains permanently thin and epithelial, as does the roof of the third ventricle and that of the posterior part of the fourth ventricle, and in Lampreys of the aqueductus sylvii as well.

Curiously enough—for what reason it is difficult to understand—the condition in which the cerebral pallium consists of a thin epithelial layer is regarded as secondary. By all the ordinary tests which are applied in speculations of this kind—viz., embryonic development and general diffusion of the character in the lower Vertebrata and absence in the higher, it should surely be regarded as a primitive character. Indeed, if we may be allowed to indulge in a little speculation of this kind, it would appear from development that the whole medullary canal at one time had purely epithelial walls, and there appears to be a tendency to the retention of this character along the middle dorsal line throughout life in all Vertebrata.

To return to the pineal body. It is developed as a diverticulum of the hinder part of the roof of the thalamencephalon. Its terminal portion becomes the pineal body or epiphysis; its proximal part is the pineal stalk. The terminal part sometimes gives rise on its anterior wall to an outgrowth which is called the *parietal* organ. The parietal organ may be developed separately from the brain roof just in front of or by the side of the epiphysis.\* It is not always formed, and usually vanishes with later growth; but in Lampreys and Lizards it

\* On account of this fact it has been suggested that the epiphysis is really a paired organ, one of the pair becoming the actual epiphysis (pineal body) of the adult, and the other either degenerating or becoming

persists and assumes a peculiar structure resembling that of the retina of the eye. For this reason it has been called the *pineal eye*. In Lampreys the pineal body also assumes the same structure. A great deal of significance has been attached to the curious eye-like structure which is assumed by the parietal organ. It has been regarded as the vestige of an unpaired eye. In our opinion the resemblance to an eye is accidental, but for a discussion of the question we refer the reader to the account of the parietal organ in the section devoted to Reptilia.

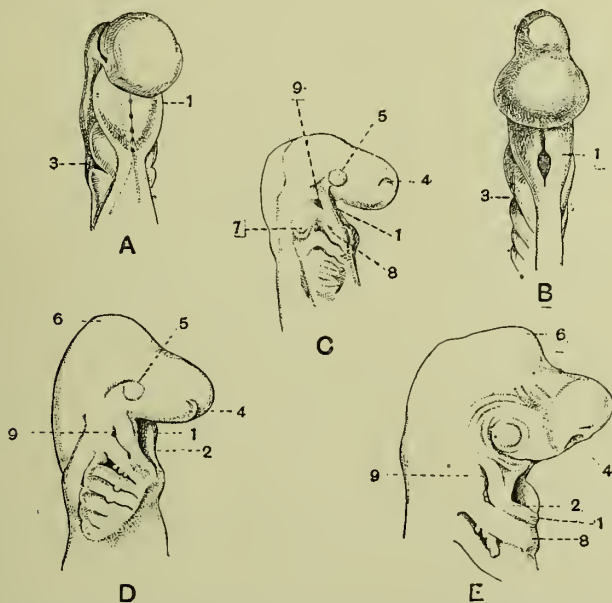


FIG. 39.—Heads of young Elasmobranch embryos (*Scyllium canicula*) (after Sedgwick). A. Ventral view of head of embryo, 7 mm. in length, with two open pharyngeal clefts. The mouth is present as a longitudinal groove in the ectoderm of the buccal depression. B. Same view of a slightly older embryo; the buccal groove has become a longitudinal slit. C. Side view of head of embryo, 9 mm. in length, with three open slits. D. Side view of head of embryo, 11 mm. in length; rudiments of external gills have appeared on the hyoid and on the first and second branchial arches. E. Side view of head of embryo of 16 mm.; external gills have appeared on mandibular arch and the angle of the jaw is marked. 1 mandibular arch; 2 angle of jaw; 3 second pharyngeal cleft; 4 nasal pit; 5 eye; 6, midbrain; 7, auditory sac; 8 hyoid arch; 9 spiracle.

The superior commissure is a small nervous development in the otherwise epithelial roof of the third ventricle just in front of the attachment of the pineal stalk. The posterior commissure, the so-called parietal organ (pineal eye). See Dendy, *Q. J. M. S.*, 42, 1899, p. 111. This view is supported to a certain extent by the arrangement in the lamprey (see p. 106).

which probably belongs to the mesencephalon, is just behind the attachment of the pineal stalk.

The *paraphysis* is the recess in the roof of the cerebrum caused by and just in front of the *velum transversum*. By some morphologists it is regarded as a special glandular organ, the secretion of which passes into the ventricle. It is not always present as a distinct structure.

The pituitary body or hypophysis develops as an evagination of the front part of the buccal cavity. It is indeed the anterior part of this cavity. In Elasmobranchs the original buccal slit—for the vertebrate mouth perforation has at first the form of a longitudinally extended slit (Fig. 39)—is continued into it. It is applied to the infundibulum and eventually becomes cut off from the mouth, except in *Polypterus* and *Calamoichthys* in which the buccal opening is retained throughout life. At the point in the embryo where the pituitary rudiment meets the infundibulum there is a close approximation and partial fusion of three other organs, viz., the front end of the gut, the anterior end of the notochord, and the median part of the premandibular somite (preoral coelom). The *lobi inferiores* and *saccus vasculosus* are parts of the infundibulum, very generally present in fishes. The former are lateral diverticula or thickenings of the infundibulum; while the *saccus vasculosus*, or infundibular gland, is a glandular dilation of its end, where it is in contact with the pituitary body.

With regard to the cranial nerves, it ought to be noticed that they all arise from the walls of the mid- and hind-brain, except the olfactory and optic nerves. These come off from the pre-notochordal part of the fore-brain, and it is doubtless to them that the fore-brain owes its relatively enormous development in all Vertebrata. The other cranial nerves, from the third nerve onwards, probably all belong to the series of nerves which is continued along the spinal cord as the spinal nerves. Indications of this are shown by a careful study of the early stages of their growth, particularly in Elasmobranch embryos, in which they appear to be associated with the cephalic segments of the coelom.

These segments, for a knowledge of which we are indebted to Balfour\* and to the later researches of Van Wijhe,† are as follows: The first cranial

\* *A Monograph of the Development of Elasmobranch Fishes*, London, 1878.

† "Ueber die Mesodermsegmente und die Entwicklung der Nerven des Selachierkopfes," *Verhandl. der k. Acad. d. Wissensch. zu Amsterdam*, 1882.

segment is represented by the premandibular somite\*—an unpaired sac with epithelial walls, immediately in front of the notochord (preoral head cavity, vide p. 8). The walls of this sac give rise to all the eye-muscles except the superior oblique and external rectus, and to mesenchyme. Its cavity vanishes, as do the cavities of all the cranial segments. The nerves are the ramus ophthalmicus profundus, which develops from the nerve crest immediately in front of the trigeminal and represents the dorsal root, and the third nerve which represents the ventral root. These two roots are both connected to the ciliary ganglion (see account of cranial nerves under Elasmobranchii).

The second segment is the mandibular somite which is dilated in its dorsal muscle-plate region and extends ventrally to the lower end of the mandibular arch (collar-somite, vide p. 7). The walls of this sac give rise dorsally to the superior oblique muscle and ventrally to the mesenchyme and muscles of the mandibular arch. The nerves are the trigeminal and the fourth, the latter being regarded as an abnormally situated anterior root. The first two cranial somites were discovered by Balfour.

The third and following segments are represented only by their dorsal muscle-plate sections, the ventral portions being merged in the continuous splanchnocoel (pericardial division). These segments may be regarded as the anterior of the trunk series of *Amphioxus*. They do not apparently communicate with the ventral splanchnocoel, which in this region undergoes a pseudo-segmentation in consequence of the formation of the gill-pouches. These pseudo-segments, or hyoid- and branchial-arch cavities, open ventrally into the pericardium, of which they are a part, and were taken by Balfour for the posterior cranial segments. The first of these muscle-plates, which may be called, from its position, the hyoid myotome, is better developed than the rest and gives rise to the external rectus muscle. It was observed by Balfour. The next three, which were discovered by v. Wijhe, are very faintly marked and transient and give rise to no muscles, in correspondence with which fact may be noted the absence of ventral roots. The next three segments (seventh–ninth) are represented by well-developed muscle plates which persist and give rise to muscles. The nerves of the hyoid segment (third) are the facial (dorsal root) and sixth (ventral root). The nerves of the next three segments are supposed to be represented by the auditory, glossopharyngeal and vagus and are without ventral roots in correspondence with the absence of myotome muscles. In the last three (or sometimes more) cranial segments, dorsal roots are present only in the embryo for a short time, but ventral roots are developed, supplying presumably the myotome muscles of this region and called the occipito-spinal nerves. These were mistaken by Gegenbaur, who did not study the embryo and observe the transient dorsal roots belonging to them, for ventral roots of the vagus. The following table represents in brief the view of cranial segmentation which has just been described.†

\* There is in some forms a pair of head cavities in front of the premandibular somite. These are sometimes in communication with and developed as diverticula of the premandibular somite, but in *Acanthias* they are said to be independent of it (J. B. Platt, *Journal of Morphology*, 5, 1891, p. 79).

† The view here given takes no account of the scheme given on p. 77, according to which the cranial nerves were originally tripartite, consisting of dorsal, lateral and ventral roots. It was formulated before the modern



	Coelomic Sac	Nerve	
		Dorsal Root	Ventral Root
Cranial segment 1	Premandibular somite. Its walls give rise to all the eye muscles supplied by the third nerve.	Ramus ophthalmicus profundus.	Third nerve.
" " 2	Mandibular somite. The walls of its dorsal part give rise to the superior oblique muscle.	Trigeminal.	Fourth nerve.
" " 3	Hyoid muscle plate giving rise to external rectus muscle.	Facial.	Sixth nerve.
" " 4	Muscle plate (transient).	Auditory.	None.
" " 5	Muscle plate (transient).	Glossopharyngeal.	None.
" " 6	Muscle plate (transient).	Vagus.	None.
" " 7	Muscle plate persistent and giving rise to muscles.	None.	Spino-occipital nerves (so-called ventral vagus roots).
" " 8			
" " 9			
and sometimes more			

The spinal nerves have two roots, which unite, and the dorsal of which has a ganglion. The ganglion may, however, be placed at the junction of the two roots. The cranial nerves are in ten pairs, but there are often some small nerves—the spino-occipital nerves (miscalled ventral vagus roots)—arising from the ventral side at the hind end of the medulla. They pass out through foramina in the skull, but are perhaps better regarded as anterior spinal nerves (see above) the dorsal roots of which are not developed.

analysis of the cranial nerves, which is due to Gaskell and is there referred to, was fully developed. The later work, which is still incomplete, may very possibly necessitate a new scheme of cranial segmentation, and the groups of cranial nerves expressed by the terms fifth, seventh, ninth and tenth may possibly be found to be connected with the ventral segmentation (pseudo-segmentation of the text) of the branchial pouches, and to be independent of the mesoblastic segmentation which is so conspicuous a feature in the trunk.

For an account of a typical arrangement of the cranial nerves the reader is referred to the section on Elasmobranchii. Their arrangement in fishes differs from that in higher types, mainly on account of the presence of the lateral line sense organs. The nerves to these appear to arise from a special part of the brain, the *tuberculum acusticum*, from which the auditory nerves also arise. They are associated in their course to the periphery with the seventh and tenth nerves, and constitute the *acustico-lateralis* system. The fibres of this system which run with the fifth and ninth are derived from these two nerves. The nerves which pass from the facial roots to the fifth nerve cause an intermingling of the roots of these two nerves, which is not easy to unravel, and which is characteristic of fishes.

A **sympathetic** nervous system appears to be present. In *Marsipobranchii*, in which all the nerves are without a medullary sheath, it cannot be fully traced, but the spinal nerves give off branches which pass to the viscera, where small ganglia are found. In other *Pisces* there is a series of sympathetic ganglia which develop as outgrowths of the spinal nerves, becoming detached from the rudiments of the spinal ganglia at an early stage. These ganglia are usually connected by longitudinal commissures, but though regularly developed, their arrangement is not easy to trace in the adult. In *Elasmobranchii* \* the system tends to take a plexiform structure, and lies in the neighbourhood of the cardinal veins. There is an especially large ganglion at about the level of the ductus cuvieri; this is supplied by a number of spinal nerves, and gives off several branches, which are distributed to the viscera with the coeliac artery. The system appears not to extend into the head. In *Teleostei* there is a definite chain of small ganglia on each side of the vertebral column. In these forms it is continued into the head, where it is connected with the trigeminal nerve and ciliary ganglion, and into the tail, where it runs in the caudal canal.

The analysis of the nerves, which is the outcome of the recent work † of morphologists and physiologists, is beyond the scope of this work, but the following points may be noted here :

\* R. Chevreton, "Sur l'anatomie du système nerveux grande sympathétique des Elasmobranches et des poissons osseux." *Arch. Zool. Exp.* (2) 5, supplement.

† W. H. Gaskell, "The structure and function of the nerves which inner-

Five kinds of nerve fibres, characterised by their structure, function and distribution, may be distinguished.

1. The system of the somatic sensory (afferent) fibres. These include the largest heavily medullated fibres which terminate in the skin and myotome muscles. They pass out by the dorsal roots in the cord, and by the roots of the trigeminal in the brain; \* their ganglia being the posterior root ganglia (spinal), and the gasserian.

2. The somatic motor (efferent) system. The fibres of this system are also large and heavily medullated: they terminate in the myotome (somatic) striated muscles; i.e. the muscles derived from the muscle-plates, including those derived from the dorsal part of the mandibular and from the premandibular somites. They pass out by the anterior roots in the cord, and by the third, fourth, and sixth cranial nerves, and are without peripheral ganglia.

3. The visceral sensory (afferent) system (*communis system*). The fibres of this system are smaller, and they are distributed to the internal mucous surfaces. They leave the cord by the posterior roots, their ganglia here being posterior root ganglia. The cranial fibres of this system are present in the roots of the fifth, seventh, ninth and tenth nerves; the ganglia being the gasserian (in part), geniculate, glossopharyngeal and jugular ganglia. Their destination is mainly the mucous surfaces of the anterior part of the alimentary canal.

4. The visceral motor (efferent) system. The fibres of this system may be subdivided into (a) those which innervate the striated voluntary muscles (mesenchymatous) of the anterior part of the alimentary canal (mandibular, branchial, and facial muscles), are fairly large, and are non-ganglionated, and (b) those which supply the unstriated muscles throughout the body (blood-vessels, gut-wall, skin, etc.). The latter are small fibres, all of which pass through peripheral ganglia. The true motor-fibres to the muscles of the small intestine and anterior part of the alimentary canal and its appendages (lungs, etc.) are derived from cranial nerves, whereas the fibres to blood vessels, skin, walls of Müllerian and kidney ducts come from the spinal cord by anterior roots. The cranial nerves contain no vaso-motor fibres.

5. The acustico-lateral system (see p. 75). This system consists of large fibres and passes out exclusively in the roots of the seventh, eighth, tenth and possibly ninth cranial nerve. It is absent in the trunk and in higher Vertebrates, except in the auditory nerve, and is distributed only to the membranous labyrinth and the lateral line sense organs (lateral line, ampullae and pit organs).

From this account it will be gathered that in the head the visceral motor (efferent) fibres travel out with the visceral sensory fibres and in the case of the fifth with the somatic sensory fibres as well, the somatic motor fibres being distinct; whereas in the trunk they leave the cord with the somatic motor fibres.

vate the visceral and vascular systems." *Journal of Physiology*, 7, 1886; and "On the cranial nerves" in *Journal of Physiology*, 10, 1889. O. S. Strong, "The cranial nerves of Amphibia," *Journal of Morphology*, 10, 1895; C. J. Herrick, "The cranial and first spinal nerves of Amphibia," *Journal of Comp. Neurology*, 9, 1899, p. 157.

\* The third nerve appears to contain fibres belonging to this system (muscular sense), and it is possible that a few of them may be contained in the vagus (Arnold's nerve).

To summarise the matter Gaskell has suggested that in the primitive condition, both in brain and spinal cord, there were three rows of nerve roots: (1) a dorsal containing somatic sensory fibres, (2) a ventral with somatic motor fibres, and (3) a lateral row containing both visceral sensory and visceral motor. This condition is modified in all existing forms in the cord by the splitting of the lateral roots in such a way that the visceral sensory roots have joined (1) and the visceral motor roots (2); whereas in the brain the roots of the lateral row have persisted and the somatic sensory roots (restricted to one) have joined them, the somatic motor roots (three in number) remaining distinct. This scheme does not, however, take account of the acustico-lateral system.

The **Eyes** have a flat cornea, and a large almost spherical lens, the anterior part of which projects far out of the pupil. Movable eyelids are present in Elasmobranchii, but are absent from most other fishes. There are no lacrymal glands. The usual eye muscles are present. There is frequently a rete mirabile, the *choroid gland*, on the ophthalmic artery as it enters the eye near the entrance of the optic nerve. The processus falciformis and campanula halleri are described below under Teleostei. The eyes are much reduced and functionless in most adult Marsipobranchs and some cave-dwelling and abyssal Teleosteans. The **Auditory Organ** consists of the otocyst or membranous labyrinth, which is embedded in the side walls of the auditory region of the skull. It lies in a cavity which is closed from the cranial cavity in most Elasmobranchs, but communicates with the latter in *Chimaera*, and Teleosteans, Ganoids and *Dipnoi*. It consists (Fig. 40) of a central chamber, the *vestibule*, and of three semicircular canals opening into the vestibule. The vestibule is divided into two parts by a constriction; of these the upper is the *utricle*, the lower the *saccul*e. The semicircular canals open into the utricle while the saccul in some fishes gives off from its posterior end a process called the *lagena*, which is an incipient cochlea. In *Chimaera* and the *Squali* the ductus endolymphaticus which is given off by the saccul opens on the surface of the head.\* Both saccul and utricle contain a chalky mass of otoliths. When the lagena is well marked its papilla acustica (*pl*) becomes separate from the macula acustica sacculi and receives a separate nerve (vide account of membranous labyrinth under *Teleostei*). The membranous labyrinth enters into peculiar relations with

\* This is the remains of the aperture of invagination of the embryo.

the air bladder in some *Teleostei*, which are fully described in the account of that sub-class.

The **Olfactory Organs** are a pair of simple pits or sacs, in the

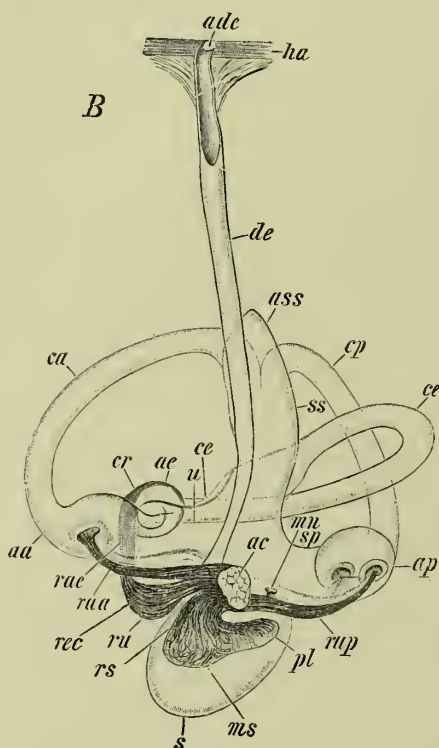


FIG. 40.—Right membranous labyrinth of *Chimæra*, seen from the median side (from Wiedersheim, after Retzius). *aa* ampulla of anterior vertical canal; *ae* auditory nerve; *ade* opening of ductus endolymphaticus; *ae* ampulla of horizontal canal; *ap* ampulla of posterior vertical canal; *ass* process of the sinus utriculi; *ca* anterior, *cp* posterior vertical canal; *ce* horizontal canal; *cr* crista acustica ampullæ; *de* ductus endolymphaticus, which opens at *ade* through the skin *ha*; *mn* macula acustica neglecta; *ms* macula acustica sacculi (the macula ac. utr. *rec* is on the other side and not properly visible); *pl* papilla acustica lagenæ (the lagena, however, can hardly be said to be present in this form); branches of auditory nerve *raa* to anterior ampulla, *rae* to horizontal ampulla, *rap* to posterior ampulla, *rec* to macula acustica utriculi, *rs* to macula sacculi and lagenæ, *ru* to macula recessus utriculi; *s* saccule; *sp* sinus utriculi posterior, *ss* sinus utriculi superior; *u* utricle.]

lining of which the fibres of the olfactory nerve terminate. In the *Marsipobranchii* the olfactory organ is partly single and presents peculiar relations (see account of *Marsipobranchii*). In other fishes each sac usually has two openings, both of which are external except in *Dipnoi*. In *Elasmobranchs* there is usually only one opening. The internal surface of the sacs is generally increased by folds of the mucous membrane.

We know practically nothing about the sense of taste. The tactile sense is no doubt specially served by the lips and their appendages, and by special parts of the appendages which are richly innervated (e.g. *Trigla*.)

The system of embedded epidermal\* sense organs which are found in all fishes requires a detailed description.

\* Lœvdig, *Lehrbuch d. Histologie des Menschen u. d. Thiere*, 1857. Solger,



In Elasmobranchs four kinds of organs are included under this head: (1) the *lateral line* proper, or *mucous canals*, with its cephalic ramifications; (2) the *ampullary* canals, or Lorenzini's ampullae; (3) *Savi's* vesicles; (4) *pit organs*. The essential

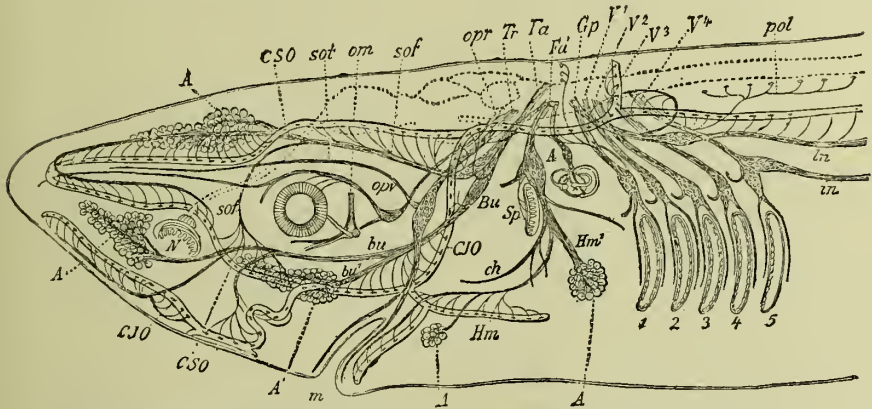


FIG. 41.—Diagram illustrating the distribution of the dorsal branches of the cranial nerves and of the lateral line canals, and the position of the groups of ampullae in an Elasmobranch (after Ewart, from Gegenbaur). *A* auditory nerve with labyrinth; it also points to the groups of Lorenzini's ampullae; *Bu* buccal branch of facial; *bu* inner branch to part of infraorbital canal, and to the inner buccal group of ampullae, *bu'* its outer branch which supplies part of the infraorbital canal, and the outer buccal group of ampullae; *ch* post-branchial branch of facial to mucous membrane, and giving off motor branches to some jaw muscles; *CSO*, *CSO* supraorbital canal; *CJO*, *CJO* infraorbital canal; *Fa*, *Fa'* roots of facial nerve; *Gp* glossopharyngeal, arising under cover of the lateralis branch of the vagus nerve; *Hm* hyomandibular canal arising from the infraorbital, and giving off the mandibular canal, the mandibular group of ampullae is in the angle between these two; *Hm'* branch of the hyomandibular nerve to the hyoid group of ampullae; *in* intestinal branch of vagus with ganglion, where it separates from fourth branchial branch; *ln* lateralis branch of vagus nerve; *m* mouth; *N* nasal sac; *om* deep branch of oculomotor giving off short root of ciliary ganglion (shown, but not marked), the long root is also shown, as are the short ciliary nerves to the eye; *opr* root of ophthalmicus profundus; *opv* dorsal branch of same, giving off long ciliary nerves; *pol* second branch of lateralis supplying some lateral line sense organs and a row of pit organs, the first branch supplies the commissure connecting the two lateral canals, and some sense organs of the main canal; *sof* ophthalmicus superficialis facialis, which supplies the supraorbital canal, and the superficial ophthalmic group of ampullae; *sot* ophthalmicus superficialis trigemini; it arises from the gasserian ganglion; *sp* spiracle; *Tr* trigemini; *V<sup>1</sup>*, *V<sup>2</sup>*, *V<sup>3</sup>* the first three branchial branches of the vagus nerve, each with a ganglion and with pharyngeal, prebranchial and post-branchial branches; *V<sup>4</sup>* the united fourth branchial branch of vagus and intestinal branch; 1-5 gill-slits.

part of these organs seems in all cases to be sensory patches of the epidermis, consisting of sensory cells, bearing short sensory hairs, and of supporting cells.

Neue Untersuchungen zur Anatomie der Seitenorgane der Fische, *Arch. f. mic. Anat.*, 1879-80. Allis, Anatomy and Development of Lateral Line system in *Amia*, *Journ. Morphology*, 2, 1889. Fritsch, *Die electrischen Fische*, Leipzig, 1890. Ewart, The sensory canals of *Laemargus*, *Trans. Roy. Soc. Edinburgh*, 37, p. 59, 1891; and The sensory canals of the skate, *Ibid.* Pollard, The lateral line system in Siluroids, *Zool. Jahrb.* 5, 1892. Cole, On the cranial nerves and lateral sense organs of fishes, *Trans. Linnean Soc.*, 1898.

In the lateral line system these sensory patches are modifications of the lining epithelium of a canal, which extends the whole length of the body and on to the head, where it branches in a somewhat complicated manner. The canals lie in the dermis or deeper in the subcutaneous tissue, and their walls contain either stiff connective tissue or cartilage (skates) for the purpose of keeping them permanently open. They communicate at intervals with the exterior by tubules. The trunk section of the canal usually lies at the junction of the dorsal and ventral divisions of the lateral muscles. The sense organs and the tubules seem to be usually metamerically arranged in the trunk, and the sense organs and tubules correspond, but in the head the metameric arrangement is of course out of the question, and the sense organs appear to be more numerous than the tubules.

That this system has originated from a skin groove is indicated by its development and by the fact that in some Elasmobranchs it has the form of an open groove throughout life. In *Chlamydoselachus* it has the form of a groove guarded by overlapping scales. In *Chimaera* it is also an open groove, though in the head the lips of the groove tend to approximate over the sense organs (Fig. 42.) In *Heptanchus* it is a groove in the greater part of the trunk, but closes into a canal in front and on the head. The course of the cephalic portion in a typical case is shown in Fig. 41. The lateral canal on reaching the head is connected with its fellow of the opposite side by a cross canal—the *commissural canal*—which may pass in front of or behind the openings of the otocysts. A short distance in front of this it branches into a canal passing above the eye—the *supraorbital canal* (*CSO*) and one passing below the eye, the *infraorbital canal* (*CJO*). The supraorbital canal extends to the front end of the snout and then passes back to join the infraorbital canal. The infraorbital canal gives off a branch back to the hyoid region, called the *hyomandibular canal* (*Hm*), which itself gives off a branch to the mandible. In *Chimaera* (Fig. 42) the arrangement is very similar.

In skates the hyomandibular canal is enormously extended backwards in a loop which lies partly on the dorsal and partly on the ventral surface of the pectoral fin, and communicates with the exterior by rather long tubules. In the same animal the lateral line canal near the head gives off

two long canals which pass backwards and outwards on the dorsal side of the fin; the anterior of these anastomoses with the dorsal part of the above described extension of the hyomandibular canal.

The whole of this system of canals is in Elasmobranchs supplied by the facial nerve and the *lateralis* branch of the vagus, which probably belongs to the facial system (see account of cranial nerves under Elasmobranchii and Fig. 41).

The ampullary canals or Lorenzini's ampullae, are unbranched canals (Fig. 43), opening, usually in groups, on the surface of the head and ending internally in vesicles—the ampullae—which are beset with radial dilatations (Fig. 44). The ampullae are placed in groups, the position of which in a typical case is shown in Fig. 41.

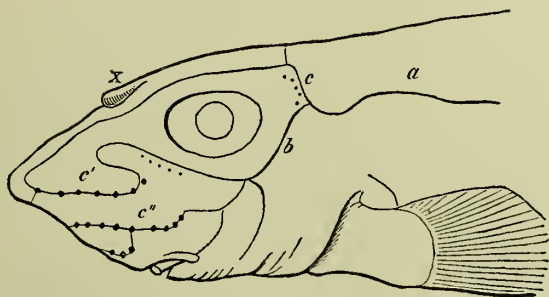


FIG. 42.—Cephalic lateral line of *Chimaera* (from Gegenbaur). *a* lateral groove of trunk, *b*, *c'* infraorbital, *c* supraorbital groove, *c'* supraorbital grooves; passing back to join infraorbital; *x* frontal appendage.

The sensory epithelium is confined to the ampullæ to which the nerves, in all cases branches of the facial, are distributed. The tubes and ampullæ contain a gelatinous matter.

Savi's vesicles are found in *Torpedo* round the electrical organs. They are completely closed.

The pit organs, found in many Elasmobranchs are sense organs sunk in pits on different parts of the head and trunk, and are supplied by the facial nerve, the lateralis of the vagus, and the trigeminal.

In Teleosteans, Ganoids and Dipnoi the lateral line system and the pit organs alone are present. The lateral line has an arrangement very similar to that described for Elasmobranchs,

but the canal wall is sometimes ossified, especially on the head, and the ossifications may be fused with the dermal and cranial bones. Very often the canal traverses the scales and bones, and

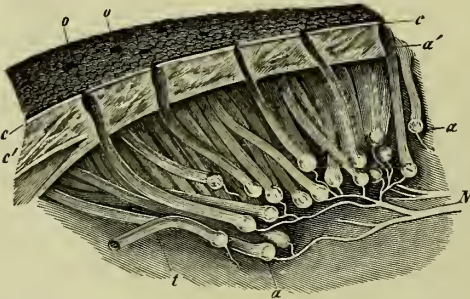


FIG. 43.—A portion of the snout of *Scyllium* in section, showing ampullary tubes (from Gegenbaur). *N* nerve; *a* ampullae; *c* epidermis; *t* tubes; *c'* dermis; *o* openings of the tubes; *a'* passage of a tube through the dermis.

the sense organs are contained in the osseous tissue. In such cases the lateral tubules, which are in some cases branched, their openings forming so-called cluster pores, perforate the bone, as does the nerve going to the sense organs. In this way certain scales on the body and bones of the head may acquire a special relation to these organs. Pit organs are present both on the trunk and head and often lie along the course of the main canals. In a few cases (*Esox*, *Gobius*, *Liparis*, etc.) the cephalic canals are alone present, the sense organs in the trunk being isolated and not connected by a longitudinal canal. In a few cases the longitudinal canal may have the form of a groove for a part of its extent. The openings of the lateral tubules may occur between the scales as well as upon them.

In addition to the innervation found in Elasmobranchs the glossopharyngeal frequently sends a branch to a few of the posterior cephalic sense organs; and it has been stated that the ophthalmicus superficialis trigemini also takes part, but this must be regarded as doubtful. In any case the nerves innervating this system of lateral line sense organs can always be traced to the special centre in the brain from which the auditory nerve arises. The pit organs are innervated by the trigeminal as well as by the facial and lateralis of the vagus.

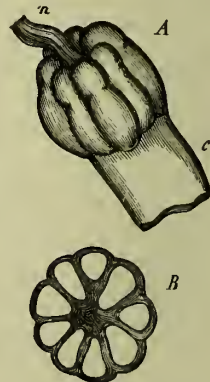


FIG. 44.—Lorenzini's ampulla. *A* from the side with nerve *n* and portion of tube *c*; *B* in section (from Gegenbaur).



**Electrical organs**,\* the function of which is to develop considerable quantities of electricity, are found in some fishes. They occur in different parts of the body and in fishes belonging to quite different groups (e.g. *Torpedo* and *Hypnos* among Elasmobranchs, and *Gymnotus* and *Malapterurus* among Teleosteans).

They differ both in structure and position in the body, but they always consist of peculiarly modified cross-striped muscular tissue.

In *Torpedo* (Fig. 45) they are placed between the branchial pouches and the anterior cartilages of the pectoral fins, and occupy the whole space between the dorsal and ventral integument. They consist of

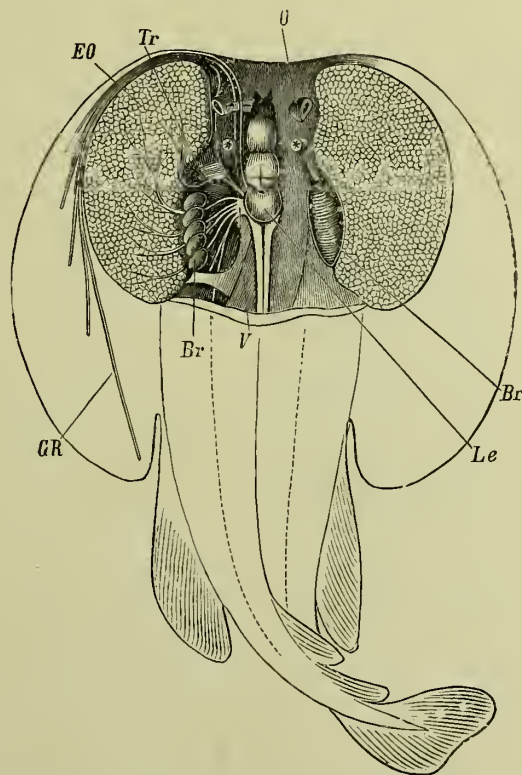


Fig. 45.—*Torpedo* with electric organ *EO* and brain exposed (after Gegenbaur), dorsal view. On the right side the dorsal surface only of the organ is exposed; on the left the nerves which supply it are shown. *br* branchial sacs; *Gr* sensory canal tubes of the skin; *Le* electric lobe of the brain; *o* eye; *Tr* trigeminal nerve; *V* vagus nerve.

of connective tissue, and divided by horizontal septa of the same material into a number of compartments placed one

\* Fritsch, *Die electr. Fische*, Abt. 1 and 2, Leipzig, 1890. Ballowitz, *Electr. Organ v. Torpedo*, *Arch. f. mic. Anat.*, 42, 1893. Sanderson and Gotch, *Elect. Organ of Skate*, *Journ. Physiology*, 10, 1889. Ewart, *Electric Organ of Skate*, *Phil. Trans.*, 1888 & 1892.



above the other. Each compartment is filled with gelatinous tissue, through the middle of which runs a horizontal plate composed of a finely granular nucleated substance and of numerous nerve-endings. This is the electrical plate. The electrical plates correspond to a certain degree to the copper and zinc elements of the voltaic pile, the gelatinous matter representing the moist intermediate layers; while the connective tissue framework serves to hold the parts together and to carry the blood-vessels and nerves. The face of the plate on which the nerves ramify is the same in all the columns of the same organ, and is always electro-negative, the other surface being positive. In *Torpedo* the nerve enters on the lower surface of the plates, the

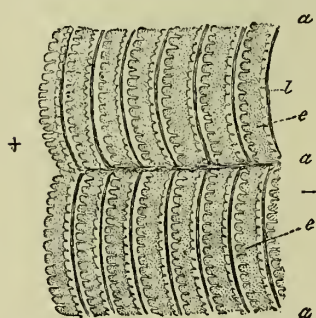


FIG. 46.—Longitudinal section through two columns of the electric organ of *Gymnotus*. *a* horizontal partition; *l* transverse partition walls, convex headwards; *e* electric plates (from Gegenbaur, after Max Schultze).

upper surface is therefore electro-positive. The organ is supplied by five strong nerves, of which the anterior is a branch of the facial, the four posterior being branches of the vagus group.

In the electric *Teleostei* the electric organs are placed in the trunk and tail, and are supplied by spinal nerves. They are similarly constituted, but the columns are horizontally placed. In *Malapterurus* they lie along the body beneath the skin, and the

posterior surface of the plates, the surface on which the nerve enters, is electro-positive. This apparent exception is explained by the fact that the nerves pass through the plate and are distributed on the anterior surface, which is electro-negative. In the electric eel (*Gymnotus electricus*) the electric organ lies at the side of the tail, and consists of long horizontal columns (Fig. 46).

The so-called pseudo-electric organs found in the tail of *Raja* and of *Mormyrus* have a similar structure, but manifest only feeble electric phenomena. They constitute a very good example of an organ which is practically of no use to its possessor, and which we should entirely fail to understand the meaning of were it not for the cases in which the electric organ is fully developed.

VASCULAR SYSTEM.—The blood is generally red; it is white

only in the Leptocephalidæ (larvæ of the eels) ; it circulates in a closed vascular system, in which a muscular pulsating region or heart is present. The heart (Fig. 47) is placed far forward on the throat, ventral to the branchial framework, and is enclosed in a pericardium, the cavity of which communicates with the body cavity in some Plagiostomes, *Chimaera*, *Acipenser*, etc. It is a simple venous branchial heart, and is composed of a sinus venosus, a thin-walled large auricle and a very powerful muscular ventricle. The sinus venosus receives the venous blood returning from the body, and the ventricle forces it through the ventral aorta to the respiratory organs. The aorta begins with a bulbous swelling (*bulbus arteriosus*) which in the *Ganoids*, *Plagiostomes* and *Dipnoi* is replaced by an independently pulsating part of the heart, with rows of semi-lunar valves (*conus arteriosus*). While the fishes with a simple non-muscular bulbus arteriosus have but two semi-lunar valves at its origin, the above-mentioned orders usually have two or four, or rarely five, rows of three, four, or more valves each, in the conus arteriosus. The aorta at once divides into a number of paired vascular arches, corresponding to the embryonic aortic arches. These are the branchial arteries ; they pass into the branchial arches and give off branches to form the capillary networks of the gills. From the capillary networks small vessels pass out which unite to form a larger vessel in each branchial arch (epibranchial or efferent branchial artery). The arrange-

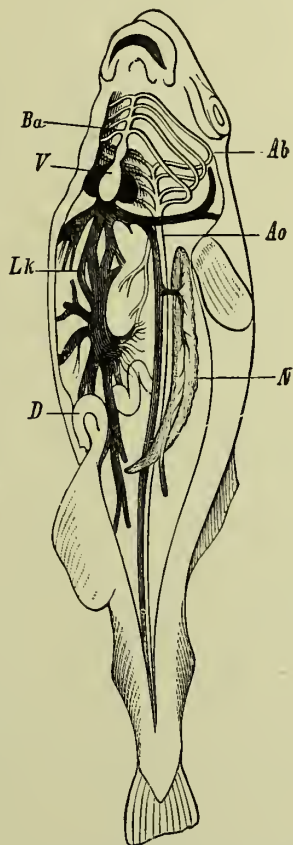


FIG. 47.—Diagram of the circulation of a Teleostean. *Ab* arterial arches ; *Ao* aorta descends into which the epibranchial arteries passing out from the gills unite ; *Ba* ventral aorta with the arterial arches which carry the blood to the gills ; *D* intestine ; *Lk* portal circulation ; *N* kidneys ; *V* ventricle. The branchial capillary system is omitted.

ment of these vessels corresponds to that of the afferent branchial arteries ; they unite to form the large aorta descendens or dorsal aorta. Before they unite the cephalic arteries pass off from the efferent vessels of the anterior arch.

The arrangement of the principal venous trunks in fishes is most nearly related to the embryonic condition. Corresponding to the four cardinal veins of the embryo, two anterior and two posterior cardinal veins bring back the blood from the anterior and posterior part of the body respectively. These veins unite on each side to form two transverse veins—the ductus Cuvieri—which enter the sinus venosus of the heart. The course of the returning venous blood is complicated by the insertion of a double portal circulation. The caudal vein does not pass directly into the posterior cardinal veins, but breaks up into capillaries in the kidneys, from which the blood passes into the posterior cardinal veins. There is thus a renal-portal circulation. For the hepatic portal circulation on the other hand the venous blood of the intestine is used ; this blood after passing through the capillaries of the liver is returned to the heart by one or more veins, which open into the sinus venosus between the two ductus Cuvieri. Such capillary systems must be a considerable hindrance to the circulation of the blood and explain the development of the so-called accessory hearts on the caudal vein of the eel and on the portal vein of *Myxine*.

The **urinogenital organs** are described under the different subclasses. With regard to them the following general remarks may be made. A pronephros is present and functional in the larva of all fishes except *Elasmobranchii*, in which there is no larval stage. It has been maintained, and a great deal has been written on the subject, that there is a vestige of a pronephros in the embryos of Elasmobranchs ; but if there is it is very feebly developed and never possesses a glomerulus.

The pronephros is the anterior and first developed portion of a longitudinal gland, which extends, in the embryo at least, the whole length of the body cavity from the pericardium to the hind end. This extended excretory organ consists of nephridia, which in Elasmobranchs are developed, as was first shown by Sedgwick,\* from the portions of the body cavity which connect the lower ends of the muscle plate cavities with the general body

\* *Q. J. M. S.*, 20, 1880, p. 164.

cavity. These portions of the body cavity are called *nephrotomes*, and accurately correspond at first with the segments of the embryonic muscular system. The pronephros is the anterior end of this excretory organ, which is developed before the rest to meet larval needs. The serial homology between the pronephros and the hinder part of the excretory system was for many years denied, partly because of a certain difference in structure and partly because there is usually a gap between it and the front end of the rest of the organ. But the differences in structure are very small, in some cases indeed (e.g. *Lepidosteus*) do not exist; and vestigial nephridia have been found in the gap between the two organs (cf. especially Price's researches on the development of the excretory organs of *Bdellostoma*). Finally, Brauer's recent researches on the development of the excretory organs of *Gymnophiona* remove all doubt on the point.

The hinder part of the excretory system differs from the pronephros mainly in the fact that the glomerulus—the vascular tuft which secretes the fluid part of the urinary excretion—is segmented into portions, one for each nephridium (or kidney tubule), instead of forming a continuous structure as in the pronephros; and the portion of the body cavity containing each of these is partly shut off from the rest to form the malpighian body of the kidney tubule. This malpighian capsule, however, frequently, though not always, retains its connection with the rest of the body cavity by the so-called nephrostome. The internal opening is retained in most Elasmobranchs, but is lost in Teleostei, Dipnoi, Ganoidei and Marsipobranchii. This hinder part of the excretory system becomes in Elasmobranchii much reduced in front and largely developed behind. In consequence of this it is described as consisting of the *mesonephros* in front and the *metanephros* behind; but this differentiation is not found in other fishes.

As in all Vertebrates, the longitudinal duct (archinephric duct) is the first part of the excretory organs to appear. The pronephros is developed in connection with the front end of this duct, so that the duct is at first the pronephric duct. The Müllerian duct is found in all Pisces with the probable exception of the Marsipobranchii and the Teleostei, and in all cases it becomes the oviduct in the female, but is reduced in the adult male. In Ganoids the longitudinal duct joins the oviduct (Müllerian)



before opening externally, but in Elasmobranchii the two ducts open separately into the cloaca. The development of the Müllerian duct is known only in Elasmobranchii. It there arises in connection with the first establishment of the longitudinal duct as an evagination of the parietal mesoderm of one of the anterior nephrotomes, so that it at first consists simply of a funnel-shaped opening of the longitudinal duct into the body cavity. It soon, however, by a process of gradual shifting, comes to open further and further back into that duct until it acquires an independent opening into the cloaca.

The female genital glands, which are, as is usual in Vertebrates, specialised patches of the lining of the coelom, and of the unsegmented \* portion of it called the splanchnocoel which persists as the general body-cavity, dehisce their ova into the body cavity, whence they escape by the Müllerian ducts—except in Marsipobranchii and Teleostei. These exceptions however are doubtful. In Marsipobranchs the genital pores by which they escape may be Müllerian ducts, though it must be confessed that there is not much to be said for so regarding them. In Teleostei the ovaries are generally saccular and continued directly into their ducts, but in some families they discharge into the body cavity and the eggs are taken up by two funnel-shaped structures which join each other and open behind the anus. It is quite possible, though not definitely proved, that these funnels are short Müllerian ducts, and that the ducts in the more usual condition, in which they are continuous with the walls of the ovary, are also Müllerian ducts, which have spread round the ovary or fused with the edges of a peritoneal recess into which the ovary has sunk.

The male gonads also are specialised patches of the coelomic lining, but the Marsipobranchii alone retain the primitive condition of testis dehiscing into the general body cavity, escape being made by genital pores of unknown homology.

In all others the testis is continuous with its duct. In Teleosts this continuity is very like the continuity found in the female between the ovary and its duct, and the homology of the male duct in these animals is not understood. It may be a per-

\* The contention which has been put forward in some quarters that the gonads of Elasmobranchs arise from the segmented part of the coelom cannot be seriously maintained.



sistent Müllerian duct which has fused with the testis or it may be something else. In other *Pisces*, with the apparent exception of the Ganoid *Polypterus*, the testis has come to consist of tubules which are connected by means of a network of tubes, called the testicular network, with some of the kidney tubules. The connection may take place along the greater part of the length of the kidney, as in *Lepidosteus* and *Acipenser*, or it may be confined to the anterior region (mesonephros), as in Elasmobranchs, or finally, as in Dipnoi, it may only occur through the hind end of the kidney. The connection is usually through the malpighian bodies of the renal tubules, but in *Amia* the tubes from the testis join the renal tubes beyond the malpighian bodies. In *Polypterus* alone is there no connection with the kidney, the testis duct passing directly back from the testis to join the longitudinal duct near the cloaca. This condition in *Polypterus* is not understood any more than is the condition of the male Teleostean, though theories have been put forward to account for it. It may be that in these forms the Müllerian duct has acquired a connection with the male gonad and persisted; or it may be that the connection is really effected through a part of the kidney which has lost all kidney structure, as has happened in some male Amphibia and in the higher Vertebrata. A study of development can only settle the question, and that has not yet successfully been made.

To return to the longitudinal duct. This, as explained above, is called at first the pronephric duct, except in Elasmobranchs, in which it is called the *segmental duct*, there being no functional pronephros. Later, when the kidney is formed and the pronephros has atrophied, it becomes the kidney duct. In Elasmobranchs, in which the kidney differentiates into meso- and metanephros distinguished, not by any break in continuity, but by size and by the course of the so-called collecting tubes of the nephridia (see below), it is called the *mesonephric duct*, because it appears to be related more especially to the mesonephric portion of the kidney. Inasmuch as in the male Elasmobranch this mesonephric duct is chiefly concerned with carrying off the spermatozoa which pass, as has been described above, through a part of the mesonephros, it is also called the vas deferens. In the higher classes of Vertebrata the mesonephric duct is called the Wolffian duct in the embryo, and persists in the male adult as the vas

deferens, but disappears or is reduced to a slight vestige in the female.

In Elasmobranchs the longitudinal duct is at first called the *segmental* duct on the view that the Müllerian duct is segmented off it. As we have seen, this is not a good description of what happens, and the name is not a happy one. After the Müllerian duct has become distinct from it, it becomes the duct of the persisting kidney, and eventually, owing to the shifting back of the point of opening of the metanephric tubules, the mesonephric duct.

The nephridia typically open directly by the so-called collecting tubules into the part of the longitudinal duct opposite to them, but with the differentiation of the metanephros the collecting tubes of the posterior nephridia shift their point of opening into the longitudinal duct backwards, so that they all come to open close together into the longitudinal duct—now called mesonephric duct—close to the cloaca. They are usually referred to as *ureters*.

The development of the nephridia of the part of the kidney behind the pronephros, as direct transformations of a portion of the coelom occurs only in Elasmobranchs. In other fishes the development of these tubules is delayed until the myotomes and adjacent tissues have become functional, and have lost their primitive relations. The consequence is that the development is modified and the nephridia (except of the pronephros) are developed from small nodules of growing tissue, which make their appearance during larval life in the proper positions.

Abdominal pores, as distinct from generative pores, are present in most Elasmobranchs, some Teleostei and in Ganoids, but they are strangely variable in their occurrence. They never act as generative outlets, and their function would appear to be for the outlet of excretory substances of the body-cavity itself. As Bles has pointed out, they are rarely present in forms in which the nephrostomes of the kidneys are persistent.

**Generative Organs.**—Excepting in certain forms, such as *Serranus* and *Chrysophrys*, which are hermaphrodite, fishes are of separate sexes; the two sexes sometimes present external differences. The male and female reproductive organs often resemble one another so closely in form and position that it is necessary to investigate their contents in order to dis-

tinguish the sex, especially as external sexual differences are frequently absent.

Copulatory organs are only found in male Elasmobranchs, in the form of long grooved cartilaginous appendages (claspers) of the pelvic fins.

Most fishes are oviparous ; only a few Teleosteans, as *Ditrema*, *Zoarces*, the *Cyprinodonta*, etc., and a great number of the sharks, bear living offspring, which for the most part undergo their embryonic development in a dilated part of the oviduct, which serves as an uterus. Reproduction usually takes place only once in the year, most frequently in spring, more rarely in the summer, and exceptionally, as in many of the Salmonidae, in winter. Many fishes, especially the males, undergo changes of colour and develop growths of skin at the spawning time. The two sexes often assemble in great shoals and seek out shallow places near the banks of rivers or near the sea coast (Herrings) for spawning. Some make more extended migrations and pass in large shoals over great distances along the sea-coast (Tunny-fish). Others leave the sea and pass up the mouths of rivers, and overcoming great obstacles (Salmon leaps) make their way up into the smaller streams, in which they deposit their spawn in sheltered places where the food is plentiful (anadromous, as the Salmon, Sturgeon, etc.). The Eels, on the other hand, migrate from the rivers into the sea, and in the following spring the young Eels enter the fresh waters by millions and pass up stream (katakadromous). The spawn is as a rule fertilized in the water, and thus artificial fertilization and pisciculture are rendered possible. In the viviparous fish, and in the Rays, Chimaera, and Dogfishes, which lay large eggs enclosed in a horny shell, a true copulation, and an internal fertilization of the egg takes place. It is worthy of note that in a few exceptional cases the male undertakes the charge of the brood (*Hippocampus*, *Cottus*, *Gasterosteus*).

The embryonic development of fishes is principally distinguished from that of most higher Vertebrates by the fact that neither amnion nor allantois are developed. Both the small eggs of the Teleosteans, which are provided with a micropyle, and the large eggs of the Elasmobranchs, which are surrounded by a hard horny case, contain a large quantity of food yolk, and undergo a partial segmentation. The eggs of Cyclostomes, Ganoids and Dipnoi, however, undergo a total segmentation. As a rule

the young fishes leave the egg-membranes tolerably early, with more or less distinct remains of the yolk-sac, which still projects externally, like a hernia. Although the body form of the just-hatched fish differs essentially from that of the adult animal, no sudden metamorphosis takes place save in a few exceptional cases.

Most fishes live in the sea, and the number of their species and genera increases as we approach the equator. But they are not all exclusively confined to fresh or salt water. Many, as the Plagiostomes, live almost entirely in the sea; others, as the *Cyprinidae* and *Esocidae*, are confined to fresh water, but there are also fish which periodically change their habitat, especially at spawning time. Some fish live in subterranean waters, and are blind, like the inhabitants of caves (*Amblyopsis spelaeus*). Few fish are able to live any length of time out of water; as a rule the wider the gill-slits the quicker does the fish die on dry land. Fishes with narrow gill-slits (Eels) possess an uncommon tenacity of life out of water. According to Hancock, a species of *Doras* migrates in great shoals over the surface of the ground from one piece of water to another. Except the Dipnoi, certain East Indian freshwater fish, the upper pharyngeal bones of which are hollowed out into the form of a labyrinth (Fig. 38) and form a multicellular reservoir for water, are capable of living the longest time out of water (*Anabas scandens*). There are even fishes which can float through the air (*Exocoetus*, *Dactylopterus*).

Marine fishes may be distinguished into shore fishes, pelagic fishes, and deep-sea fishes, which, as in the case of marine and fresh-water fishes, graduate into one another. Shore fishes live near the surface, and do not descend to any great depth; they are comparatively restricted in range. Pelagic fishes inhabit the surface waters of the ocean, where they usually spawn, though some visit the shores for this purpose; they are usually strong swimmers and wide ranging, but a few (e.g. *Hippocampus*, *Antennarius*, etc.) are poor swimmers, and infest floating seaweed, or drift on the surface. Some pelagic fishes come to the surface at night only, descending in the daytime to a considerable depth (*Brama*, *Sternoptychidae*, *Scopelus*, *Astronesthes*). The largest fishes belong to the pelagic fauna, e.g. *Rhinodon*, *Selache*, *Carcharodon*, *Myliobatidae*, *Thynnus*, *Xiphiidae*, *Orthogoriscus*. The features of deep-sea fishes are referred to below.

Owing to the uniformity of the conditions of life in the abyss in different parts of the world, they are probably for the most part wide ranging.

The greatest depth at which fishes are known to exist is 2,900 fathoms. Many littoral fish descend periodically within the limits of the deep-sea fauna, but these are not conspicuously modified. Fishes which habitually live at a depth of 80-120 fathoms, have a black lining to the pharynx and large eyes. Fishes which belong to the real deep-sea fauna all present very similar characters, those from 300 fathoms being as much modified as fishes from 2,000 fathoms. The principal changes in external conditions to which deep-sea fishes are subjected as compared with surface forms are (1) absence of light, (2) stillness of the water, (3) constant low temperature, and (4) increase of pressure. With regard to the latter, it may be stated that pressure increases by one ton on the square inch for every 1,000 fathoms of depth. The principal bodily characters are as follows: The eyes are largely developed and luminous organs, or, to speak more correctly, organs the function of which is probably to supply luminosity are present. When the supposed luminous organs are not present the lateral line canals are much dilated, sometimes into wide cavities, and full of mucus. The eyes are, however, in some cases reduced or absent. The osseous and muscular systems are feebly developed; the bones being light and provided with little calcareous matter, and the muscles thin. When the fish are brought to the surface the bones are found to be but loosely bound together, and the body easily falls to pieces. This is probably due to the expansion of gases within the body. The air-bladder presents no special modifications, and appears to be always without a pneumatic duct, even in Physostomous forms. It is generally ruptured in fishes brought up from the deep sea, and in fishes from 80 fathoms it is much distended, and the eyes protrude and the stomach is everted. Deep-sea fishes are sometimes found floating on the surface in a dead or dying condition, and often with the stomach distended with recently swallowed prey. It is conjectured that such fishes have accidentally ascended too far above their normal depth, possibly during the struggle of swallowing their prey which may be as large as themselves, and then owing to the expansion of gases consequent on the diminished pressure have been



carried to the surface. Sharks, Rays and flat-fish (with one exception in each case) cease below 500 fathoms. Twelve hundred fathoms is the limit for *Holocephali*. The eggs of some deep-sea fishes ascend to and develop at the surface, but in other cases the development undoubtedly takes place in the abyss.

Fishes are of great importance to our knowledge of the development of animal life on the earth, owing to the frequent appearance of their fossil remains in all geological periods. In the palaeozoic formations very singular fish-forms, as the Cephalaspidæ (*Cephalaspis*, *Coccosteus*, *Pterichthys*), constitute the oldest representatives of the Vertebrata. From the palaeozoic formations to the chalk we find almost exclusively cartilaginous fishes and Ganoids, amongst which the forms with persistent notochord and cartilaginous skull predominate. Ganoids, with a fully developed bony skeleton, round scales and an externally homocercal caudal fin, appear for the first time in the Jurassic rocks, where we also find the first Teleosteans. From the chalk onwards, in the more recent formations, the Teleosteans increase in number and variety of forms the nearer we approach to the fauna of the present time.

The class Pisces is divided into the five sub-classes, Marsipobranchii, Elasmobranchii, Ganoidei, Dipnoi, and Teleostei.

## CHAPTER V.

### SUB-CLASS MARSIPOBRANCHII (CYCLOSTOMATA).\*

*Vermiform fishes with smooth scaleless skin, cartilaginous skeleton and persistent notochord; with suctorial mouth, single nasal organ, and straight intestine; without jaws, paired appendages, generative ducts, sympathetic system, and conus arteriosus. The unpaired fins are without actinotrichia (dermal fin-rays).*

The *Marsipobranchii* are vermiform in appearance, varying in length from two feet or more (*Bdellostoma*) to a few inches (*Petromyzon fluviatilis*). The skin is smooth and without scales, and the skeleton is cartilaginous and notochordal. They are without paired fins, but possess an unpaired caudal fin (*Myxinidae*, Fig. 62), to which may be added a dorsal unpaired fin in the posterior region (*Petromyzontidae*, Fig. 48). In the

\* J. Müller, *Vergleichende Anatomie der Myxinoiden*, Berlin, 1835-45. A. Günther, *Catalogue of the fishes in the British Museum*, London, 1870. C. Kupffer, Die Entwicklung der *Petromyzon planeri*, *Arch. f. mic. Anat.*, 35, 1890. P. Fürbringer, Unters. z. vergl. Anat. d. Muskulatur. d. Kopfskelets d. Cyclostomen, *Jena. Zeitsch.*, 9, 1875. W. K. Parker, Skeleton of *Petromyzon* and *Myxine*, *Phil. Trans.*, 1883, p. 373. P. Langerhans, Unters. üb. *Petromyzon planeri*, *Ber. d. naturf. Gesellsch. zu Freiburg*, 1873. A. Schneider, Beiträge, z. vergl. Anat. etc. d. Wirbelthiere, Berlin, 1879. T. H. Huxley "On the Cranio-facial apparatus of *Petromyzon*," *Journal of Anat. and Physiology*, 10, 1876, pp. 412-28. F. Ahlborn, Das Gehirn v. *Petromyzonten*. *Z. f. w. Z.*, 39, 1883, pp. 191-295, and Hirnnerven v. *Petromyzon* *Z. f. w. Z.*, 40, 1884, pp. 286-308. G. C. Price, Ontogenie d. Myxinoiden *Bdellostoma stouti*, *Sitz. ber. Math.-phys. Klasse d. k. bayer. Akad. d. Wiss.*, 26, 1896, Munich. Id. Development of excretory organs of *Bdellostoma stouti*, *Zool. Jahrbuch. Anat.*, 10, 1897, p. 207. W. F. R. Weldon, The head-kidney of *Bdellostoma*, *Q. J. M. S.*, 24, 1884, p. 171-182. J. W. Spengel, Die Excretionsorgane von *Myxine*, *Anat. Anz.*, 13, 1897, p. 49-60. F. C. Studnicka, Sur les organes pariétaux de *Petromyzon planeri*, *Vestník České Spol. Nauk Prag*, p. 1-50, 1893. J. D. Ogilby, "A Monograph of the Australian *Marsipobranchii*," *Proc. Lin. Soc. N. S. W.*, 21, 1896, p. 388-426.

*Petromyzontidae* and in the tail of myxinoids the fins are supported by cartilaginous somactids. They possess a suctorial mouth, which is without jaws, but is provided with horny teeth. By means of it, with the assistance of a suctorial tongue-like structure they attach themselves to and suck their prey. *Myxine* indeed bores its way into the body cavity of other fishes, and is truly parasitic. The nasal aperture is single, and leads into an unpaired nasal sac. In this and in other features of their anatomy, which will be described later, they are unique amongst Vertebrates. Nevertheless, we shall not follow the example of some zoologists who have established the *Marsipobranchii* as a separate class of the *Vertebrata*, distinct from the class *Pisces*. We hold them, in spite of the remarkable and unique features of their organization to be true *Pisces*, not only

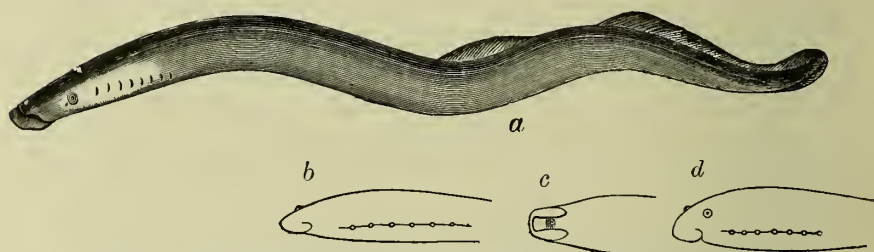


FIG. 48.—a. *Petromyzon fluviatilis* (after Heckel and Kner). b, c, d, stages in the transformation of *Ammocoetes branchialis* into *Petromyzon planeri* (after v. Siebold); b head of an eyeless larva, side view; c the same, ventral view; d later stage with small eyes, side view.

by their aquatic habit of life, but by the characters of their respiratory and vascular organs. They possess a simple tubular heart, which distributes the blood by means of a ventral aorta to the walls of the gill pouches; and these open to the exterior on the sides of the body in the ordinary piscine manner. In the structure of their mouth parts they present some resemblance to the larvae of anurous *Amphibia*, but the resemblance is too vague to permit of any definite approximation to that group in classification.

The *Marsipobranchii* fall into two main groups which present marked points of difference from one another. These are the *Petromyzontidae* or lampreys, and the *Myxinidae* or hag-fishes. In the *Petromyzontidae* the nasal sac does not communicate with the mouth, the eyes are normally developed, and possess eye-muscles with their corresponding nerves, the pericardium does

not communicate in the adult with the abdominal part of the body cavity, and the pronephros does not persist. In the *Myxinidae* the nasal sac does communicate with the alimentary canal by an aperture which perforates the roof of the mouth, the eyes are much reduced and without the muscles and the corresponding cranial nerves, the pericardium communicates with the general body cavity by a wide opening on the right side, and the pronephros is persistent in the adult. Moreover, the *Myxinidae* possess a contractile dilatation on the portal vein (portal heart) which is not present in the lampreys.

The skin is slimy, and has the usual vertebrate structure. It possesses unicellular glands which secrete the mucus. In the *Myxinidae* there is in addition on each side of the body and embedded in the subcutaneous tissue, a row of segmentally arranged slime-glands, which open on the surface, and pour out a mucus containing an immense number of threads. These threads arise in special cells of the gland and unwind themselves when the mucus is discharged. They were discovered by Retzius and described and figured by Müller.



FIG. 49.—Thread-cell of *Myxine glutinosa* with unwinding thread (after Müller).

Nothing of the nature of lateral line sense-organs has been observed in *Myxinidae*, but in the lampreys small sensory eminences, partially sunk in pits, are found on the head and in two double rows on the body.\*

The great lateral muscles are divided up by septa, which have a zig-zag course, into myomeres of the usual piscine type. The myomeres extend on to the head to just behind the eyes. In the *Myxinidae* there is in addition a ventral sheet of obliquely directed muscle-fibres which is unsegmented. There is a complicated system of muscular bands connected with the mouth, tongue, and pharynx.

In *Petromyzon* the portion of the lateral muscles dorsal to the gill-sacs is continued to just behind the eye and contains a greater number of segments than the corresponding ventral portion. The ventral part reaches to just in front of the first gill opening. In *Ammocoetes* there is one myomere anterior to the first gill aperture; this in the adult divides up into nine or ten myomeres (Schneider).

\* Langerhans, *op. cit.*

The **skeleton** consists of cartilaginous, notochordal, and membranous tissue; there is no bone. There are two kinds of cartilage at least, the hard with considerable intercellular matrix, and the soft with but little.

The vertebral column consists of a persistent notochord with a tough sheath, which is formed of two layers, an inner somewhat fibrillated chordal sheath (or *membrana elastica interna*) and an outer thin elastic coat (*membrana elastica externa*); both are devoid of nuclei. The notochord so constituted is surrounded by a nucleated membranous sheath (the so-called skeletogenous tissue, or *membrana reuniens*), which extends dorsalwards on each side so as to enclose the spinal cord. Small cartilaginous

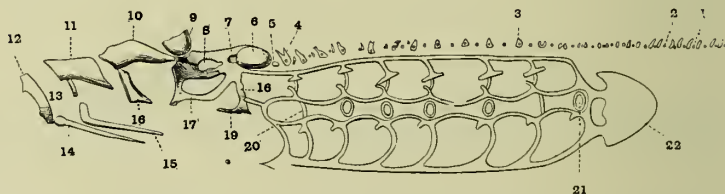


FIG. 50.—Cartilaginous skeleton of the anterior part of the body of *Petromyzon fluviatilis*; side view (after A. Schneider). 1 Foramen for sensory, 2 for motor root of spinal nerve; 3 eleventh dorsal arcualium; 4 first dorsal arcualium, pierced by the first anterior root, which passes into the ligament between the fourth and fifth myomere; 5 foramen for vagus; 6 auditory capsule; 7 foramen for trigeminal; 8 foramen for optic; 9 nasal capsule; 10 posterior dorsal cartilage; 11 anterior dorsal cartilage; 12 annular lip cartilage; 13 anterior lateral cartilage; 14 styliform cartilage of 12; 15 unpaired lingual cartilage; 16 posterior lateral cartilage; 17 subocular arch; 18 styloid process; 19 cornual cartilage; 20 branchial basket-work; 21 the seventh gill aperture (the first and sixth gill apertures are omitted); 22 pericardial cartilage.

pieces are developed on the *membrana reuniens* on each side: these, the *dorsal arcualia* (*dorsalia*), are roughly segmentally arranged.

In *Petromyzon* there are in the branchial and trunk region two pairs of arcualia in each segment, while in the tail they are fused to form on each side a continuous ridge, with which the cartilaginous fin-rays (somactids) here present are continuous. Ventralia, fused to a continuous ridge, are also present in the caudal region, and are continuous ventrally with ventral somactids. In myxinoids cartilaginous elements are restricted to *dorsalia* and somactids in the caudal region, and to some somactids in the trunk.

Anteriorly the notochord extends into the base of the skull, ending just behind the pituitary body.

The skull consists of cartilage and membrane. The roof is entirely membranous in myxinoids, but in *Petromyzon* there is a narrow bar of cartilage passing across the posterior part of the



otherwise membranous roof. In the floor there is a basi-cranial fontanelle (Fig. 52, 9) in the anterior (trabecular) region just in front of the anterior end of the notochord; this transmits the pituitary pouch or posterior nasal canal, which, passing back from the nasal capsule, ends blindly in the *Petromyzontidae* (Fig. 51, 1), but opens into the mouth in the *Myxinidae*. This canal lies between the basilar plate and the roof of the mouth. The olfactory capsule is single and attached to the anterior part of the cranium by fibrous tissue (Fig. 50, 9). The auditory

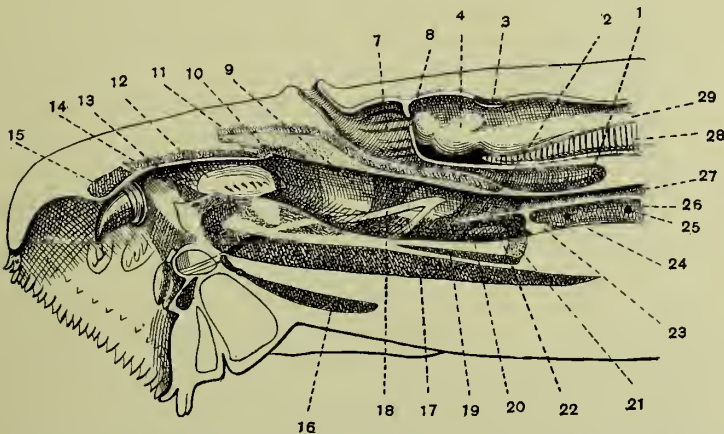


FIG. 51.—Longitudinal vertical section through the anterior end of *Petromyzon fluviatilis* (after Huxley). 1 Blind end of posterior nasal canal; 2 hinder margin of hard palate (intertrabecula); 3 cartilaginous roof of skull; 4 brain; 7 nasal capsule; 8 posterior wall of nasal capsule; 9 the anterior portion of the subocular arcade; 10 postero-lateral cartilage; 11 postero-dorsal cartilage (ethmovermerine plate); 12 tongue; 13 anterolateral cartilage; 14 anterodorsal cartilage; 15 annular lip cartilage; 16 median ventral cartilage; 17 lingual cartilage; 18 ventral division of fifth nerve coming through the subocular foramen; 19 cornual cartilage; 20 posterior part of subocular arch; 21 styloid process (hyoid); 22 tentaculate branchial valve; 23 pharyngeal velum; 24 internal opening of first branchial pouch; 25 ditto of second branchial pouch; 26 suboesophageal tube; 27 oesophagus; 28 notochord; 29 spinal cord.

capsules (Fig. 50, 6) are attached laterally in the posterior region on each side of the basilar plate. The subocular arch (Fig. 50, 17) is a ventro-lateral continuation of the basilar plate and trabecular region on each side; it contains a fenestra and is supposed to correspond to the subocular or palato-quadrate arcade of the Amphibian skull. At the point where the posterior part of this arch joins the basilar plate, there is given off ventralwards the styloid process (Fig. 50, 18, and Fig. 51, 21), the end of which in *Petromyzon* extends horizontally as the cornual cartilage (Fig. 50, 19). The styloid process and cornual cartilage have been

compared to the hyoid arch of the higher forms. In the *Petromyzontidae* the following additional cartilages are present. Attached to the anterior end of the base of the skull is a large median plate of cartilage—the posterior dorsal cartilage (Fig. 50, 10, and Fig. 51, 11). Immediately in front of this,

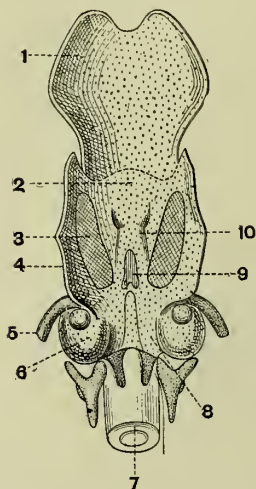


FIG. 52.—Ventral view of skull of *Petromyzon marinus* (after W. K. Parker). 1 posterior dorsal cartilage (ethmovomerine plate), formed by union of cornua trabeculae, passing behind into 2 ethmoid region, formed by union of anterior portion of trabeculae; 3 subocular fenestra; 4 subocular arcade; 5 styloid process; 6 auditory capsule; 7 notochord; 8 basilar plate or investing mass (formed by union of parachorial cartilages), showing contained notochord; 9 basi-cranial fontanelle, or space between the unfused posterior portion of trabeculae; 10 cartilage formed by fusion of middle portion of trabeculae (so-called hard palate of J. Müller); it lies between mouth and posterior nasal pouch, and corresponds to the posterior intertrabecula of myxinooids.

and overlapped by it, is the anterior dorsal cartilage (Fig. 50, 11, and Fig. 51, 14). Just below the latter there is an annular cartilage (Fig. 50, 12, and Fig. 51, 15), which lies within the lips, and from which there projects back on each side the so-called styli-form cartilages (Fig. 50, 14). The anterior lateral cartilages are paired rods (Figs. 50 and 51, 13) in relation with the anterior dorsal cartilage, and the posterior lateral (Fig. 50, 16, and Fig. 51, 10) are similarly in relation with the posterior dorsal.

Finally, in the tongue in the floor of the mouth there is a median lingual cartilage (Fig. 50, 15, and Fig. 51, 17), and ventral to this the so-called median ventral cartilage (Fig. 51, 16; not shown in Fig. 50). The lingual cartilage is also present in Myxinooids, in which it is very largely developed.

It is probable that the posterior dorsal cartilage is derived from the fused anterior end of the trabeculae and it has been suggested that the posterior lateral cartilages are the homologues of Meckel's cartilage. The anterior dorsal, and the anterior laterals, and the annular cartilages are

generally regarded as labials, while the lingual cartilage has been compared to the basi-hyal; it is connected with the styloid process (supposed hyoid) in Myxinooids (Fig. 53).

The foramen for the optic nerve is in the side wall of the skull above the subocular arch (Fig. 50, 8), that for the fifth nerve just in front of the auditory capsule (Fig. 50, 7), while the seventh

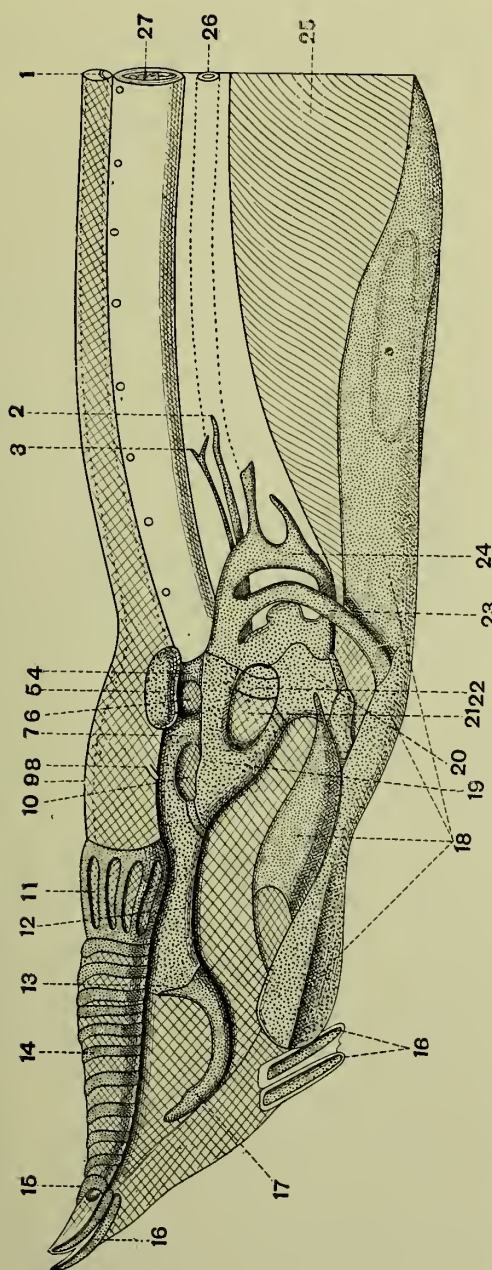


FIG. 53.—*Myxine glutinosa*, side view of dissection of fore-part of body (after W. K. Parker). 1 spinal cord; 2 process of the hinder part of the subocular arch (from just behind the oval fenestra, supposed to represent the pharyngobranchial of the first branchial arch); 3 process of the dorsal part of supposed first branchial arch; 4 fenestra between 4 and 7; 5 auditory cartilage; 6 fenestra between 4 and 7; 7 anterior part of posterior attachment of subocular arcade to skull (representing the pedicle); 8 optic nerve perforating the membranous side walls of skull; 9 membranous wall of skull; 10 subocular fenestra; 11 nasal capsule; 12 left trabecula cranii (palatine part); 13 ethmoid or region of union of trabeculae cranii in front; 14 nasal canal; 15 external nasal opening; 16 cartilages of buccal cirri; 17 anterior continuations of trabeculae in front of ethmoid, called prepalatines by Parker, corresponding to the posterior laterals of the lamprey; 18 great lingual cartilages, the different parts are variously homologised; 19 anterior part of subocular arcade; 20 posteriorly directed angle of subocular arcade; 21 oval fenestra in posterior part of subocular arcade; 22 anterior end of 2; 23 hyoid arch (styloid process); 24 first branchial arch; 25 lingual muscles; 26 pharynx; 27 notochord.

nerve passes out through the auditory capsules. The vagus nerve passes out behind the skull, between it and the first dorsal piece of the vertebral column (Fig. 50, 5).

In its general features the chondro-cranium of *Marsipobranhii* resembles that of other fishes, but is more largely supplemented by membranous structures, nearly the whole of the roof, the entire occipital region and the basicranial fontanelle being membranous. From what is known of the development of the lamprey's skull, it would appear that the basilar plate is formed by two parachordals between which the notochord lies (Fig. 52), that these become continuous above and below the notochord (below only in *Myxine*), and that to their outer sides the auditory capsules become attached. In front of the parachordals and continuous with them are the *trabeculae cranii* which always remain separate posteriorly, leaving the basicranial fontanelle, but unite in front to form in *Petromyzon* (Fig. 52) the hard palate, the ethmoid and the posterior dorsal plate (ethmovomerine plate), and in *Myxine* (Fig. 53, 13) a small median piece in front of the large basicranial fontanelle. In front of the latter there is in Myxinoids a pair of cartilaginous horns (Fig. 53, 17) which may be regarded as the homologues of the posterior lateral cartilages of the lamprey. Moreover in Myxinoids there are two median cartilages, called intertrabecular cartilages not present as separate structures in *Petromyzon*; one of these—the posterior intertrabecular—is a spoon-shaped cartilage lying in the basicranial fontanelle and underlying the naso-palatine canal; the other, the anterior intertrabecular, extends in front of this and lies beneath the nasal canal. In all Marsipobranchs there is a ventro-lateral process of the hinder part of the trabecular region (anterior lateral process) which meets and fuses with a corresponding process of the anterior end of the basilar plate or auditory cartilage (posterior lateral process, said to be comparable to the pedicle of the Amphibian suspensorium, Fig. 53, 7); thus forming the so-called subocular arcade. The subocular arcade closely resembles the same structure in the Amphibian skull, but against the comparison of the two is the fact that the ventral division of the fifth nerve passes dorsal to the arcade in Amphibians, whereas in Marsipobranchii it passes through the fenestra (Fig. 51, 18). In Myxinoids the hinder part of the subocular arcade contains two fenestrae (Fig. 53, 6, 21), which are not present in lampreys. The supposed hyoid arch arises in all Marsipobranchs from the hind end of the subocular arcade (Fig. 50, 18; Fig. 53, 23). In lampreys it ends in the expansion of the cornual cartilage (Fig. 50, 19) and is not connected with the lingual (15) which is the supposed median element of the hyoid arch. In Myxinoids it joins the great lingual cartilage (Fig. 53, 18) which consists of several parts. In the same group the hinder part of the subocular arcade also gives off close to the point of origin of the hyoid a bar of cartilage which passes ventralwards just within the hypoblastic epithelium to join the subocular arch lower down (Fig. 53, 24). This structure is not represented in lampreys and is supposed to be the first branchial arch. The velum in *Myxine* is supported by some pieces of cartilage which are in connection with the upper end of this supposed branchial arch (Fig. 53, 2, 3).

In Myxinoids the brain lies entirely above the cartilaginous skull, which is a mere floor, the side walls and roof being entirely formed of membrane. Moreover in Myxinoids the angle of the subocular arcade is posterior (Fig.



53), *i.e.* the palatine process of the trabecular region is directed backwards and not merely outwards as in lampreys (Fig. 50). Further the labial cartilages of the lamprey, viz. the anterior dorsal, the anterior laterals and the annular are not present in Myxinoids. On the other hand the oral barbules of the Myxinoids contain a cartilaginous axis and the lingual cartilage is enormously developed (Fig. 53), and connected with the styloid process (supposed hyoid arch).

In the *Petromyzontidae* there is a branchial basketwork of cartilage placed superficially, near the skin and supporting the outer parts of the branchial passages. It consists (Fig. 50) of eight irregularly curved bars of cartilage placed between the successive gill sacs.\* They are connected dorsally by a longitudinal band of cartilage, which lies along the notochord sheath and is continuous with the hind end of the skull, and by three other longitudinal bands, of which two are lateral, one being above and one below the branchial apertures, and one is ventral and partly fused with its fellow. The branchial basket is continuous posteriorly with a cartilaginous cup which supports the wall of the pericardium (Fig. 50, 22). The first branchial aperture is behind the first bar, and the seventh or posterior in front of the last bar.

The branchial basketwork is supposed to be developed in the somatopleure and not to be homologous with the branchial arches of other fishes which lie in the gutwall. The only representative of these structures in Myxinoids (in addition to the supposed traces of mandibular and hyoid arches) is the structure described above as the first branchial arch (Fig. 53, 24).

**The alimentary canal.** The mouth, or buccal funnel (Fig. 54), is suctorial and armed with horny epidermic teeth; in the lamprey it is surrounded by a lip carrying short papillae, in *Myxinidae* by eight barbules (Fig. 61). On the ventral side of the mouth is the tongue, which, moving backwards and forwards like a piston, enables the animal to attach itself by its mouth as by a sucker. The tongue carries teeth (two rows in the myxinoids on the supralingual cartilages), which enable it to inflict considerable wounds upon its prey. The buccal funnel leads into a tube, which is supposed to be stomodeal, and may be called the buccal cavity. This is continued behind into the oesophagus,

\* There appears to be some variation in the details of the arrangement of the branchial basketwork in the different species (cf. W. K. Parker's account with Schneider's figure).



which passes back through the pericardial cavity to become continuous by a valvular aperture with the straight intestine, which opens at the anus. The anterior end of the intestine is slightly dilated, and receives the opening of the bile-duct, and in *Petromyzon* the intestine is provided with a longitudinal fold or valve, which takes a slightly spiral course.

In Myxinoids the naso-palatine canal (pituitary pouch) opens into the hinder part of the buccal cavity. This may be taken to mark the junction of mouth and pharynx. The opening is guarded by an epiglottis-like valve and directly behind there is a velar membrane of a peculiar form hanging from the dorsal wall and supported by the so-called pharyngo-branchial cartilages (Fig. 53, 2, 3). The part of the alimentary canal immediately succeeding the mouth and receiving the internal gill apertures should be called pharynx, though it is commonly termed oesophagus. In *Petromyzon* a velar fold marks the junction of the suboesophageal tube or bronchus with the hinder part of the mouth.

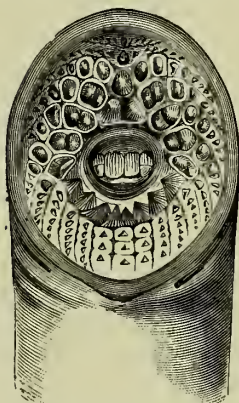


FIG. 54.—Head of *Petromyzon marinus*, seen from below showing the lip and horny teeth of the buccal funnel.

There is a gall bladder, but in the adult *Petromyzon* the bile-ducts and gall-bladder atrophy and the liver cells become filled with fat (Schneider). A pancreas and spleen appear to be absent, and the mesentery is very imperfectly developed. The anus is placed in the median ventral line in a shallow pit immediately in front of the urogenital opening.

The respiratory organs consist of a number of branchial sacs, in which the branchial lamellae are contained. In *Petromyzon* there are seven pairs of these sacs, and each of them opens independently to the exterior in the anterior region of the body, by a short external branchial passage (Fig. 48), but internally they open into a longitudinal suboesophageal tube (bronchus), which opens into the buccal cavity in front (Fig. 51), and ends blindly behind. The anterior opening of the suboesophageal tube is guarded by a membranous velar fold.

In *Myxine* there are six pairs of branchial sacs (seven have been observed in rare cases). In *Bdellostoma* the number is more variable; seven pairs appear to be the usual number, but

there may be six pairs, or seven on one side and six on the other (heterotrema), or there may be more than seven (up to fourteen pairs). In both genera the sacs are connected directly with the oesophagus (pharynx) by internal branchial tubes, and with the exterior by external branchial tubes, but whereas in *Bdellostoma* each of the external branchial passages opens separately by a small aperture (Fig. 61), in *Myxine* all the external branchial tubes of the same side are directed backwards, and unite together before opening to the exterior by a common opening at the hind end of the branchial region. In both genera there is on the left side a tube, the oesophageo-cutaneous duct, which leads directly from the oesophagus behind the last gill sac, to open with the external branchial tube of the last left gill sac in *Bdellostoma*, and with the left gill aperture of *Myxine*. The oesophageo-cutaneous duct is much wider than the external branchial tubes.

In all Marsipobranchs respiration can be effected while the animal is adhering to foreign objects by the suctorial mouth. In *Petromyzon* respiration is effected by taking in water through the external branchial openings into the branchial sacs, and then expelling it again by the same way. In Myxinoids the water is said to enter through the nasal tube, which communicates with the mouth through the posterior nasal passage, and passes out by the branchial sacs; but the nasal passage is a narrow one, and perhaps hardly sufficient to supply all the respiratory water. Moreover, it would not be available when the animal's head is buried in the tissues of its prey. It would appear more probable that some at least of the inspiratory water enters through the oesophageo-cutaneous duct.

In *Petromyzon* the branchial basket plays an important part in respiration. In expiration it is compressed by the transverse muscles; in inspiration it recovers by its own elasticity. In *Myxinidae* it is possible that the huge lingual apparatus may play some part in bringing about inspiratory dilatation of the pharynx, but it has been asserted that the inflow of water in these animals is effected through the nasal canal by ciliary action.

In the respiration of *Ammocoetes* water is taken in through the mouth and passed out by the clefts. The expulsion of the water is effected by muscular constriction of the branchial region; the

inspiration by the dilatation of the branchial region caused by the elasticity of the branchial basketwork. The double valve (velar fold) at the junction of the mouth and branchial portion of the alimentary canal prevents the regurgitation of water in expiration.

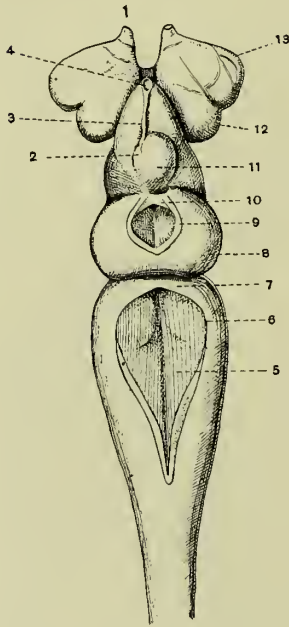


FIG. 55.—Dorsal view of the brain of *Petromyzon fluviatilis* (after Ahlborn). 1 olfactory nerves; 2 left ganglion habenulae (the two pineal bodies have been removed); 3 continuation of 2 along the roof of the third ventricle; 4 swollen termination of 3 which is connected with the ventral of the two pineal bodies; 5 fourth ventricle; 6 edge of thin roof of fourth ventricle; 7 cerebellum; 8 optic lobes; 9 edge of thin roof of iter; 10 posterior commissure; 11 right ganglion habenulae; 12 cerebral hemisphere; 13 olfactory lobe.

In *Petromyzon* it has been observed that in every inspiratory and expiratory movement of the muscles of the branchial region water is at the same time taken in and expelled from the nasal opening.

The **central nervous system** is constructed on the usual vertebrate type. The brain of *Petromyzon* (Fig. 55) is unique amongst *Vertebrata* for the fact that the median part of the roof of the sylvian aqueduct (*iter*) is epithelial and covered by a choroid plexus. Moreover, the cerebellum is very small, and the thalamencephalon of some length. The third ventricle divides in front into a right and left canal, each of which, passing laterally, gives off a branch backwards into the cerebrum and forwards into the olfactory lobe. The pineal body, or epiphysis, consists of two vesicles, lying, the one dorsal to the other, over the anterior part of the thalamencephalon. The larger dorsal

vesicle is the pineal body proper, the ventral smaller one being called the parietal organ. The dorsal vesicle lies close beneath the skull-wall, and is the so-called pineal eye. The ventral part of its walls contains a white, sometimes a black, pigment, and presents a structure which recalls that of the retina. It is connected by a solid stalk (pineal stalk) containing nerve-

fibres with the right of two thickenings on the superior commissure, called the right ganglion habenulae. The ventral and smaller vesicle also presents in its lower wall, though not so markedly, features which recall retinal structure. It is hollow and is connected with a small solid body on which it lies, and which is the anterior part of the small left ganglion habenulae (Fig. 55, 3). These two bodies, though in contact, are apparently not connected. The pineal stalk is connected to the roof of the brain just in front of the posterior commissure, while the parietal organ is attached just anterior to the superior commissure. The pineal body lies close to the roof of the skull, and the skin above it is not pigmented (Fig. 56).

The hypophysis or pituitary body is dorso-ventrally flattened and follicular in structure. It lies beneath the infundibulum.

In Myxinoids the corpora bigemina are present in the normal form and there is no thin place in the roof of the iter. The thalamencephalon is not nearly so prominent, the optic lobes being approximated to the cerebral lobes. The anterior part of the brain is solid, the central canal not extending beyond the mid-brain. A small space in the region of the thalamencephalon may be made out but it is quite isolated from the iter. A pineal body, has, so far, not been found in the myxinoid brain.

The **cranial nerves** are fairly normal in their arrangement. There are ten pairs, but in Myxinoids the third, fourth and sixth appear to be entirely absent, in correspondence with the absence of eye-muscles. The optic nerves, which are very small in Myxinoids, appear not to cross, the chiasma being hidden in the substance of the brain. In *Petromyzon* the sixth nerve arises close to the fifth, and supplies the inferior rectus as well as the external rectus. There is said to be no lateral line branch of the vagus in Myxinoids, but in the lampreys this nerve is well developed and reaches to the end of the tail. It is, however, in an unusual position, being placed far from the skin close to the neural sheath of the vertebral column, and it appears to be connected with the posterior roots of the spinal nerves dorsal to which it passes.

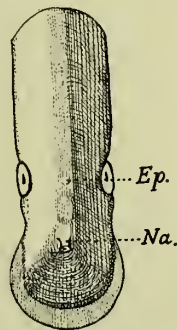


FIG. 56.—Dorsal view of the head of *Petromyzon planeri* (after Ahlborn). *Na* external nasal aperture; *Ep* position of the epiphysis (the non-pigmented character of the skin at this spot is not clearly shown).



The fifth nerve divides into two branches, the ophthalmic\* which is purely sensory and passes to the skin on the head, and the ventral

branch, which is both motor and sensory. The ventral branch divides into an external and internal branch, which do not correspond to the superior and inferior maxillary branches of other fishes, for they both supply muscles which in Selachians are supplied by the inferior maxillary branch.† The seventh nerve is in *Petromyzon* a purely sensory nerve; in *Myxinidae* it is mainly sensory.

The vagus arises by eight roots, of which the four anterior group themselves together as a nerve which by its distribution to the tissue between the first and second branchial pouches must obviously be compared to the glossopharyngeal (Fig. 57, *Br*<sub>1</sub>). The other four vagus roots unite in a ganglion which is joined by a commissural branch from the seventh nerve (*vi*<sub>1</sub>-*x*) and gives off dorsally the *lateralis* (lateral line branch) and ventrally the visceral branch. The latter supplies the branchial region and the whole length of the intestine in the wall of which it lies. In the branchial region in *Petromyzon*, and possibly in the intestinal region as well, the visceral branch of the vagus is connected with the posterior roots of the spinal nerves. As suggested by Müller, it very possibly represents the *sympathetic* which is otherwise absent in Marsipobranchs.

Some ventral roots arise behind the vagus (so-called ventral vagus roots) and unite to form a nerve

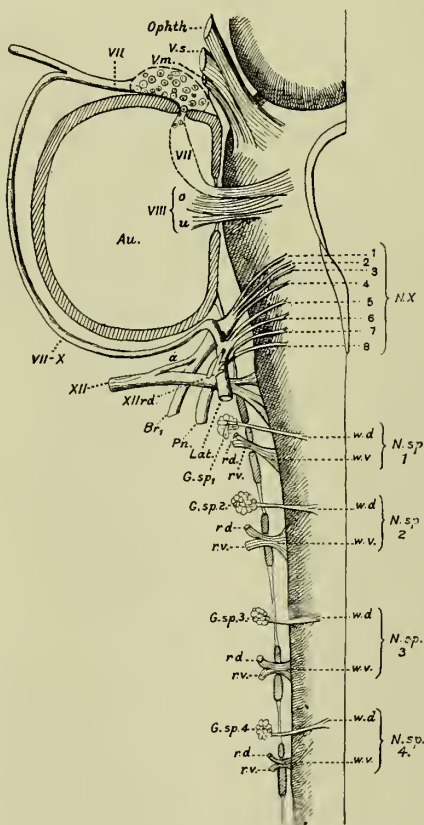


FIG. 57.—Diagrammatic dorsal view of the posterior cranial nerves of *Petromyzon* (after Ahlborn). *a* Sensory root of hypoglossal from the glossopharyngeal; *Au* auditory capsule; *Br*<sub>1</sub> glossopharyngeal; *G. sp. 1*, *G. sp. 2* etc., ganglia on posterior roots of spinal nerves; *Lat.* lateral branch of vagus; *N. X.* vagus roots (including those of the glossopharyngeal); *N. sp.* spinal nerves; *Ophth.* ophthalmic branch of trigeminal; *Pn* vagus; *rd.* dorsal, *rv.* ventral ramus of ventral root of trigeminal; *vm* motor, *vs* sensory root of trigeminal; *w.d.* dorsal, *w.v.* ventral roots of spinal nerves; *VII* facial nerve; *VII-X* branch connecting facial and vagus; *VIII* auditory nerve; *XII* hypoglossal; *XII rd.* dorsal branch of *XII* to muscles of head.

\* A motor branch is mentioned by some authors.

† Fürbringer, *loc. cit.*



(xii.) which supplies the tongue muscles. It is called the hypoglossal, and gives off near its origin a branch which supplies the anterior part of the dorsal muscles.

The spinal cord is flattened ; it has neither dorsal nor ventral fissure, though traces of a dorsal fissure may be represented by a fine tract of connective tissue which passes from the dorsal side of the central canal to the dorsal surface of the cord.

The spinal nerves have dorsal and ventral roots which unite in Myxinoids, but not in *Petromyzon*. The posterior roots possess a ganglion, which lies just outside the skeletogenous wall of the neural canal. All the nerves are without the medullary sheath and the motor fibres are larger than the sensory.

In *Petromyzon* the dorsal root of the first spinal nerve enters the septum between the fourth and fifth myomeres, the ventral root divides and supplies the fourth and fifth myomeres. The motor root of the second spinal nerve supplies the fifth and sixth myomeres, while the third and subsequent spinal nerves each supply one myomere only.

**Sense Organs.** The external nostril and the nasal sac are single and median, though the olfactory nerves are double. From the ventral side of the nasal sac a tube—the *nasopalatine canal*—is continued backwards between the brain and the skull floor, passes through the basicranial fontanelle and ends blindly on the ventral side of the anterior end of the notochord in *Petromyzontidae*, whereas in *Myxinidae* the same tube opens posteriorly into the mouth. The palatal opening of this canal has nothing to do with the posterior nares of higher vertebrates. It appears to be derived from the pituitary invagination of the embryo, which arises in Marsipobranchs, not as in most Vertebrates from the mouth, but as an ectodermal invagination in front of the mouth, which secondarily becomes connected with the nasal pit. It is for this reason sometimes called the pituitary pouch.

The eyes are normal in *Petromyzon*, and possess the usual eye muscles.

In the Myxinoids they are extremely reduced and without eye-muscles. In *Bdellostoma* they are embedded in a spherical fatty mass, and placed beneath the skin which is without pigment immediately over them. In *Myxine* they lie deeper within the muscles close to the skull wall.

The eye in *Myxine* is without any trace of lens and appears to have but little if any pigment.\* It consists of little more than the much degenerated optic cup. According to Müller the optic nerve in *Myxine* passes dorsal to the ophthalmic branch of the fifth.

The auditory organ differs from that of other Vertebrata. In *Petromyzontidae* it consists of a vestibule and two semi-circular canals, in *Myxinidae* of a single semicircular canal only.

The **body cavity** is divided into two parts, the pericardial cavity and the general body cavity. These two cavities communicate by a wide opening on the right hand side in *Myxinidae*; in *Petromyzontidae* they communicate in the larva, but not in the adult. The general body cavity opens into the urinogenital sinus by two genital pores (one in *Myxine*), through which the generative products escape.

In the anterior part of the body there is a system of spacious venous sinuses. These are specially developed round the branchial sacs, and in Myxinoids round the ventral aorta, thus constituting a kind of haemocoelic body cavity for these parts.

The **vascular system** is arranged essentially in the manner usually found in fishes. The heart consists of sinus venosus, large auricle, and ventricle. There are only two valves at the junction of the ventricle and ventral aorta, and the base of the ventral aorta (*bulbus*) is much swollen owing to the large amount of elastic tissue in its walls. This *bulbus* is without any muscular tissue. There is no conus arteriosus. The branches of the ventral aorta are distributed one to each branchial sac, and the efferent branchial vessels are collected into two aortic roots which are continued forward as carotids, and unite behind to form the dorsal aorta. The dorsal aorta is also continued forward in the middle line as a carotid. In *Myxinidae* the genital vein and some veins from the anterior part of the body wall fall into the portal. Moreover, in *Myxinidae* the portal vein is dilated into a contractile sinus, which, contracting about as rapidly as the heart, drives the blood through the liver. It is a remarkable fact that no muscular fibres can be found in the walls of this portal sinus (J. Müller). The portal vein extends for some distance in the intestinal wall and has been called the subintestinal vein.

\* C. Kohl, "Rudimentäre Wirbelthieraugen," *Bibl. Zool.* (Leuckart & Chun.), 4, heft 13, 1892.

The **kidneys** are not divided into meso- and meta-nephros. They are placed along the dorsal side of the body cavity for the middle of its length, being absent at the anterior and posterior ends. The longitudinal ducts (pronephric ducts) extend along their whole length and join together posteriorly in *Petromyzon* to open by a single opening into the urogenital sinus. The urogenital sinus which also receives the two genital pores opens at the end of a papilla just behind the anus into a depression of the skin into which the anus also opens. In *Ammocoetes* the kidney ducts open into the hind end of the intestine (cloaca). The separation of the urogenital sinus and the formation of the genital pores takes place just before the metamorphosis.

In *Myxinidae*\* there is a shallow cloaca which receives the opening of the intestine in front, the wide genital pores (single in *Myxine*) on the dorsal side of the anus, and the two urinary ducts, opening close together at the end of a papilla behind.

In *Myxine* the kidneys have an exceedingly simple structure. The longitudinal ducts give off at segmental intervals short lateral tubes which open into large malpighian bodies. The glomeruli are multipolar, i.e., are connected at several places with the wall of the capsule. In *Petromyzon* the structure is very similar but more complicated, though the malpighian capsules of successive tubules are separate, the vascular tissue of the glomeruli is continuous.

The tubules of the kidney do not open into the body cavity by nephrostomata.

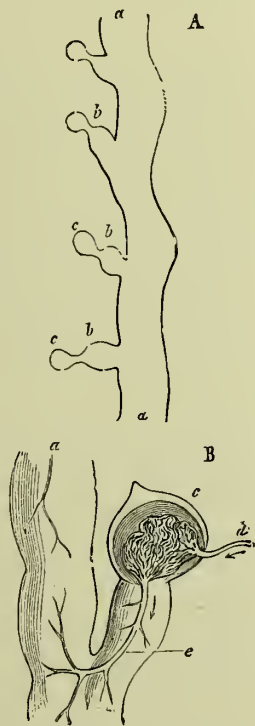


FIG. 58.—Portions of the kidney of *Myxine* (after J. Müller). B represents a portion of A highly magnified; a pronephric (longitudinal) duct; b kidney tubule; c glomerulus; d afferent, e efferent artery.

\* R. H. Burne, "Porus genitatis in *Myxinidae*," *Journ. Linn. Soc.*, 26, 1898, p. 487.

Abdominal pores as distinct from the genital pores appear to be absent.

In *Myxinidae* the pronephros persists as a lobulated organ in the pericardial cavity of the adult, and was called by Müller the suprarenal body. In *Petromyzon* it is quite absent in the adult though present in the larva.

The pronephros of *Petromyzon* is developed in the embryo and has three or four body-cavity openings and a continuous glomerulus. It is in relation with the pericardium and atrophies during the *Ammocoetes* stage. The kidney is developed in the young larva posteriorly, its anterior end being a short distance behind the pronephros. The tubules arise as excavations in the mesoblastic tissues. This larval kidney of the *Ammocoetes* atrophies after the metamorphosis and is replaced by an exactly similar structure placed further back.

The pronephros of the adult Myxinoid consists of a large number of nephrostomes which end blindly internally in a mass of lymphoid tissue, or possibly in some cases, perhaps in young specimens, open internally into an isolated anterior portion of the pronephric (segmental) duct. There is also at the hind end of this organ a glomerulus of some size projecting into an open recess of the pericardial cavity.

The whole excretory system of *Bdellostoma* \* appears to develop in the same way in which the pronephros does in other types, that is to say the longitudinal duct (pronephric) and the excretory tubules (segmental tubules) arise in continuity with each other from the body-cavity epithelium. The parts of the body-cavity into which the segmental tubes open soon become separate from the rest and form a series of small vesicles each communicating with a segmental tube. These vesicles become the malpighian bodies and the segmental tubes become the renal tubules. It is not known how the pronephric part of the system acquires the peculiar structure which it exhibits in the adult.

As stated above the persistent kidneys of Marsipobranchs show no differentiation into meso- and meta-nephros and the testes are not connected with them.

The **generative organs** are unpaired. They are attached to the dorsal wall of the body cavity by a broad membrane, and the generative products, both male and female, are shed into the body cavity, whence they escape by the genital pores. *Myxine* is hermaphrodite, and the reproductive gland produces spermatozoa before ova † (protandrous). *Petromyzon* is dioecious, but ova have been observed in the testis.

\* Price, *op. cit.*

† J. T. Cunningham, "Reproductive elements in *Myxine glutinosa*" (*Q. J. M. S.*, 27, 1887), and "Spermatogenesis in *Myxine*" (*Q. J. M. S.*, 33, 1891). The hermaphroditism of *Myxine* is denied by Dean (*Journ. Coll. Sci., Tokyo*, 19, 1904).

The **development** has been fully worked out in *Petromyzon planeri*.<sup>\*</sup> The egg is small, about 1 mm. in diameter. It is enclosed in a membrane formed of an inner perforated and an outer structureless layer. Outside there is a mucous envelope which causes the egg to adhere to foreign objects. The male adheres to the female during oviposition and the ova are deposited in a hole previously made and subsequently covered up, the fish moving stones for this purpose by means of their suctorial mouths. The eggs are laid in April and May. Segmentation is unequal but complete; the gastrula is formed by a combination of invagination and epibole, and the blastopore persists as the anus. The central nervous system is formed by a solid keel-like ectodermal ingrowth, in which the central canal arises by excavation, and there is a solid cord of cells connecting the hind end of it with the dorsal hypoblast. The pituitary body is formed from an invagination of the ectoderm and subsequently becomes connected with the nasal pit, with which its proximal part remains in communication throughout life, as the naso-palatine canal or pituitary pouch.

The young are hatched as larvae which soon become *Ammocoetes*. These live for three or four years, developing and increasing in size until they become as large as or larger than the adult. They then undergo a sudden (in three or four days) metamorphosis (from August to January) and become adult (Fig. 48). The adult possesses ripe generative organs and spawns in April-May. After spawning the lamprey (in the case of *P. fluviatilis* at least) dies.

*Ammocoetes* was formerly regarded as a distinct genus of animal, and separate species were distinguished. The fact that it becomes metamorphosed into *Petromyzon* was discovered two hundred years ago by L. Baldner, a fisherman of Strasburg, and rediscovered by Aug. Müller.<sup>†</sup>

In *Ammocoetes* the buccal cavity is without the annular lip, but possesses a semicircular upper lip (Fig. 59), and a small separate lower lip. There are no teeth, but several fringed barbels surround the mouth. The eyes are imperfect and hidden beneath the skin. The gill openings are placed in a groove on each side. The median fin extends all along the back, as a continuous structure. The branchial pouches open into the pharynx directly, and there is no suboesophageal tube or bronchus distinct from the pharynx. In *Ammocoetes* there is a gall bladder and bile duct, which opens into the intestine. In the lamprey both these structures are absorbed, and the intestine itself undergoes partial atrophy. The eye in *Ammo-*

<sup>\*</sup> F. M. Balfour, *A Treatise on Comparative Embryology*, vol. ii. 1881 (with literature to date). A. E. Shipley, *Q. J. M. S.*, 27, 1887. C. Kupffer, *Arch. mic. Anat.*, 35, 1890. P. Bujor, "Metamorphose de l'*Ammocoetes branchialis*," *Rev. Biol. Nord. France*, iv. 1891, p. 41.

<sup>†</sup> Müller's *Arch.*, 1856, p. 325.



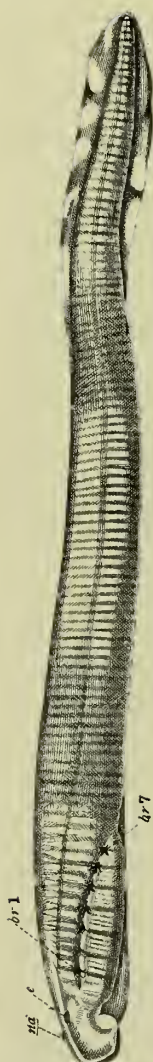


FIG. 59.—A. *Ammocoetes* of *Petromyzon planeri*, 2 ins. long, side view (after W. K. Parker) br1 first, br7 seventh branchial aperture; na nasal aperture; e eye.



B Ventral view of the head of the same larva.

*coetes* is only partly developed and lies beneath the skin. In the lamprey it becomes fully developed and travels to the surface. The pericardium of *Ammocoetes* opens into the general body cavity, but the two become completely separate in the adult. The anterior part of the kidney which had been developed in the *Ammocoetes* disappears, and a fresh posterior part is formed. The pronephros had already begun to disappear during the *Ammocoetes* stage, and the portion of the cloaca into which the urinary ducts open becomes separated off as a urogenital sinus shortly before the metamorphosis.

The skeleton undergoes very considerable change at the metamorphosis. The *Ammocoetes* is without the cartilaginous dorsalia or neural arches in the trunk region. These appear at the metamorphosis as do cartilages of the mouth, and the side walls and roof of the skull. The spinal cord, which is nearly round in section in *Ammocoetes*, becomes flattened at the metamorphosis.

The head muscles of *Ammocoetes* are entirely destroyed and reformed at the metamorphosis.

The thyroid body arises in the embryo as a groove in the branchial region of the pharynx. The opening soon becomes narrowed to a pore placed between the second and third permanent\* branchial pouches (Fig. 60). In *Ammocoetes* the tube so formed becomes divided and assumes

\* There is said to be a trace of an eighth pouch, in front of the first permanent one, in the embryo and young larva. It is supposed to represent the hyomandibular cleft of other fishes, but it never acquires gill folds or an external opening.

a very complicated glandular form. After the metamorphosis it is less conspicuous and appears to be without the opening into the throat.

In *Myxinidae* the eggs are very much larger (19 mm.  $\times$  7 mm. in *Myxine*, 31 mm.  $\times$  9.5 mm. in *Bdellostoma*) and contain a considerable quantity of yolk. They are enclosed in a horny case with hooked processes proceeding in tufts from each end. The egg case appears to be the vitelline membrane.

The *Ammocoete* lives buried in mud and sand and likes dark places. It lives on small aquatic organisms (*Infusoria*; *Daphnia*, Rotifers, etc.). The marine lamprey ascends rivers at spawning time, sometimes carried by the salmon or shad (*Alausa vulgaris*), to spawn. They eat worms and small aquatic animals. The *Myxinidae* live exclusively on other fishes. They are able by their formidable dental armature and powerful lingual muscles to make their way into the body cavity of their prey; in which they are sometimes found embedded.

The Marsipobranchii are sometimes spoken of as a degenerate group. We do not think that there is any evidence of degeneration. The most important points in which they differ from other fishes relate to the skeleton, and to the nasal organ. But these are precisely the organs which show the greatest amount of variation within the group as at present constituted. This seems to point to the fact that they separated off from other fishes at a time when these two organs were in a highly indeterminate condition, and had not attained to that fixity of structure which characterises on the whole the general arrangement of the skeleton, and nasal and pituitary sacs in other fishes.

The condition of the eyes in *Myxinidae* might be held to be evidence of degeneration, but we should rather be inclined to regard it again as the survival from a time when the visual organ was more variable and had not obtained that fixity of character which it has at the present day. No

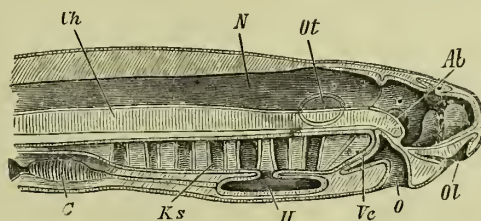


FIG. 60.—Diagrammatic longitudinal section through the head of a larva of *Petromyzon* (after Balfour). *Ab* optic vesicle; *C* heart; *Ch* notochord; *H* thyroid involution; *Ks* branchial pouches; *N* nervous system; *O* mouth; *Ol* olfactory pit; *Ot* auditory vesicle (represented as visible); *Ve* velum.

doubt many individuals were then produced with imperfect visual organs. Most of these naturally died out in competition with their more highly endowed brethren, but in some cases compensating advantages in other organs enabled them to hold their own in spite of their defective sight. To hold that a free-living animal, and a myxinoid must after all be regarded as such, can lose its eyes through disuse would seem to be an impossible position. The absence cannot be considered as other than a disadvantage to it.



FIG. 61.—Ventral view of anterior end of *Bdellostoma forsteri* (after W. K. Parker) *br. p.* external apertures of branchial sacs; *d. oe* opening of ductus oesophageus cutaneus.



FIG. 62.—*Myxine glutinosa* (Règne Animal).

Fam. 1. **Petromyzontidae** (*Hyperoartia*), lampreys, nine-eyes. With seven external gill apertures on each side which lead into a sub-pharyngeal tube opening anteriorly into the pharynx and ending blindly behind, and with a complete branchial basket-work. The suctorial mouth is surrounded by a circular lip and is provided with horny, simple or multicuspid teeth, without barbules. The single nasal opening is in the middle of the upper side of the head, and the nasal duct (pituitary sac) ends blindly behind. Eyes are present. With two dorsal fins, and a spiral valve in the intestine; gall-bladder absent. The eggs are small, and there is a prolonged larval stage in which the young are known as Ammocoetes. Fresh waters and coasts of the temperate regions of both hemispheres. *Petromyzon* Art. coasts and fresh-waters of the northern hemisphere; *P. marinus* L., sea-lamprey; *P. fluviatilis* L., river-lamprey. *Ichthyomyzon* Girard, west coast of North America; *Mordacia* Gray, without gular pouch, coasts of Chile, south-east Australia and Tasmania, entering fresh-water to breed; *Geotria*, Gray, with gular pouch, rivers of Chile, south and south-east Australia and New Zealand; *Velasia* Gray, without gular pouch, is an immature stage of *Geotria*.

Fam. 2. **Myxinidae** (*Hyperotreta*). Nasal aperture single, at the anterior end of the body; the nasal duct (pituitary sac) opens posteriorly into the pharynx and has cartilaginous rings; mouth suctorial, without lips, with barbules, with one median palatal tooth and two rows of lingual teeth; branchial openings far behind the head, lead directly into pharynx; branchial basket-work not present; a series of mucous sacs on each side of the body; eyes hidden under the skin, and very imperfect, without lens or

muscles ; intestine without spiral valve ; gall bladder present ; egg large with horny case provided with threads for adhesion ; marine in temperate regions of both hemispheres. *Myxine* L., hag-fish, with six pairs of branchial sacs opening by one external opening on each side. *Bdellostoma* J. Müll. (*Homea* Fleming), with six or more (up to fourteen) branchial

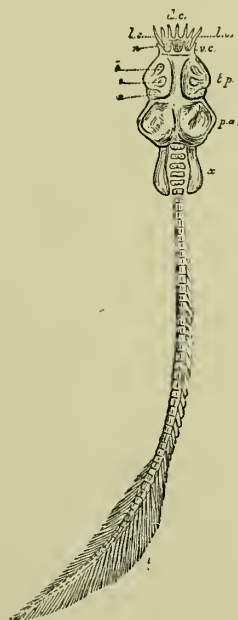


FIG. 63.—*Palaeospondylus gunni* ventral view of head and side view of vertebral column. *tp* trabeculo-palatine part of skull ; *pa* parachordal part of skull ; *a c, l.c, v.c.* oral cirri ; *a, b, c, n* markings of more uncertain significance ; *x* post occipital plates (from S. Woodward).

apertures on each side, each leading to a branchial sac ; the number of branchial sacs may be different on the two sides of the body ; southern hemisphere. *Palaeospondylus* Traquair, from the old Red Sandstone of Scotland, is supposed to be a fossil Marsipobranch with calcified cartilaginous endoskeleton (Fig. 63). The notochordal sheath appears to have contained rings.

## CHAPTER VI.

### SUB-CLASS ELASMOBRANCHII.\*

*Fishes with a cartilaginous endoskeleton, placoid scales, and abdominal pelvic fins provided with claspers in the male. There is a conus arteriosus, an optic chiasma and a spiral valve in the intestine. There is no air-bladder. The eggs are large, and, except in Laemargus, provided with a horny case. In the embryo the gills project from the gill clefts as filaments.*

The Elasmobranchii or cartilaginous fishes include the sharks and rays. With the exception of one or two sharks and a few rays they are entirely marine forms. They are remarkable for possessing more features which are embryonic in the higher purely terrestrial Vertebrata than any other group of fishes. Of such may be mentioned the oro-nasal groove, the opening between the membranous labyrinth and the exterior, the uncovered gill apertures, the open spiracle, the cartilaginous skeleton, the opening between the pericardium and the body cavity. Lastly they are the only fishes which possess eggs containing so much yolk that the whole development is embryonic.

Only two species of shark are known to be exclusively inhabitants of fresh-water (*Carcharias nicaraguensis* and *gangeticus*), but several ascend large rivers, *e.g.*, the Tigris and Ganges, to a considerable distance. Most Selachians are pelagic or shore forms, and some descend to great depths (*Scyllium* has been taken at 700, *Chlamydoselachus* at 100-150, *Centroscyllium* at 245, *Pristiurus* at 500, and *Centrophorus* at 345-500

\* See Günther, Day, Jordan and Evermann, Bridge, Boulenger, cited under *Pisces*; J. Müller and J. Henle, *Systematische Beschreibung der Plagiostomen*, Berlin, 1839. F. M. Balfour, *Development of Elasmobranch Fishes*, London, 1878.



fathoms). Their flesh is not usually esteemed as food, but some of them are eaten by poor people.

The body is elongated and spindle-shaped in the *Squali*, the anterior part being somewhat broad and depressed dorso-ventrally as compared with the narrower posterior region; in the *Raji* it is strongly compressed dorso-ventrally. In some forms, mostly in the *Raji*, the snout is prolonged to a greater or less extent. This is most markedly the case in the saw-fish shark *Pristiophorus*, and in the saw-fish *Pristis*. In the hammer-heads the anterior part of the head is elongated transversely, the eyes being placed at the ends of the prolongations. The median fins are typically two dorsal, a caudal, the ventral part of which is divided by a notch into two parts, and an anal placed between the caudal and the anus. The paired fins are well-developed; the pelvic being smaller than the pectoral,

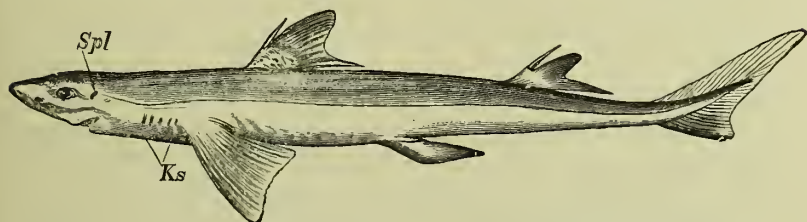


FIG. 64.—*Acanthias vulgaris*. *spl* spiracle; *ks* gill slits (from Claus).

and abdominal in position. In the males the pelvic fins are provided, each with a copulatory appendage—the clasper (*pterygopodium*, *mixipterygium*), which is grooved on its dorsal side, the groove leading into a cavity at the base of the appendage. In the *Raji* the pectoral fins are very large and their line of attachment to the body has a considerable antero-posterior extension. The muscular system is on the usual piscine type. The great lateral muscle is divided into a dorsal and ventral half, the myomeres of which alternate. There is the usual system of branchial and mandibular muscles.

The gill-clefts are tubes usually five on each side (in *Chlamydoselachus* and *Hexanchus* there are six, in *Heptanchus* seven), and their external openings which are placed laterally in *Squali*, ventrally in *Raji*, are not covered by an operculum (Fig. 64). Internally they open into the pharynx and their walls are pro-

vided with a number of lamellate folds of the mucous membrane, which are placed on their anterior and posterior walls (except in the last tube, which has no branchial lamellae on its posterior wall), and are attached through their whole length (Fig. 118), not projecting freely as do the pectinate gill processes of *Teleostei*. In addition there is usually an anterior tube leading outwards from the pharynx and opening externally on the dorsal surface close behind the eye. This opening is called the *spiracle* and the tube itself must be regarded as belonging to the series of branchial tubes of which it is the first. It differs from these, however, in never possessing branchial lamellae, though it often has traces of these as a few small folds of the lining of its anterior wall, which constitute the *pseudo-branch* or mandibular gill of these fishes. In the embryo long filaments—the so-called external gills—project from all these openings including the spiracle; they are in reality externally projecting internal gills.

In *Raji* the spiracle is much larger than in *Squali* and it doubtless allows of the entrance of water into the pharynx when the animal is lying flat upon the ground or partly buried in sand. In *Squali*, in which it is very variable, being sometimes absent and nearly always small, its function is not clear. In some species in which it is very small it may be present or absent in different individuals. It is sometimes present in embryos of forms in which it is absent in the adult (*Carcharias*), but whether this is always the case is not known. From the fact that it is smaller than the posterior branchial apertures even at its first appearance (which is subsequent to that of the others) it may be presumed that it is usually absent in such cases, but the matter wants looking into. When it is absent in the adult and present in the embryo, it is without projecting gill filaments in the embryo (Müller): In *Scyllium*, *Pristiurus*, *Mustelus*, etc., the spiracle gives off a diverticulum to the auditory cartilage of the skull.

The nasal apertures and mouth are almost always placed on the ventral surface of the head (in *Chlamydoselachus* the mouth is anterior and the nasal apertures are dorsal), usually at a considerable distance from the front end. The nasal apertures are frequently connected with the mouth by a groove, the oro-nasal groove, and sometimes they are so close that their openings are confluent with the mouth. In other cases they are at some distance from the mouth and there is no oro-nasal groove. The anus (cloacal opening) is placed between the pelvic fins, and there are two abdominal pores, one on either side of the anal opening, which lead into the body-cavity.

Abdominal pores vary considerably.\* In some species they are absent altogether, in others they are present in the adult, while in yet others they are present in some individuals and not in others. Their external opening is always on an ectodermal surface, either just outside the cloacal boundary, or into a cloacal pouch, which is a diverticulum of the proctodeal part of the cloaca.

The eyes are usually provided with upper and lower cutaneous folds which represent eyelids, and in some forms there is a third inner eyelid or nictitating membrane which can be drawn over the eye.

The otocysts retain their communication with the exterior by means of a canal, the *aqueductus vestibuli*, which opens on the dorsal surface throughout life (p. 77). The lateral line is a canal which extends in the skin from the very hind end of the body to the head, where it branches out to different parts in the usual piscine manner (p. 80). It opens to the exterior at intervals. In addition to the system of the lateral line, there are the openings of the so-called ampullary canals. These are placed in groups in the head (Lorenzini's ampullae, p. 81). Luminous organs† irregularly scattered over the body are found in many pelagic members of the *Spinacidae* (e.g., *Spinax*, *Laemargus*, *Isistius*) in the form of minute cutaneous patches which probably secrete a luminous mucus.

The skin is tough and rough owing to the presence of a vast number of placoid scales. These are rhombic bony plates embedded in the cutis and carrying a small spine, which

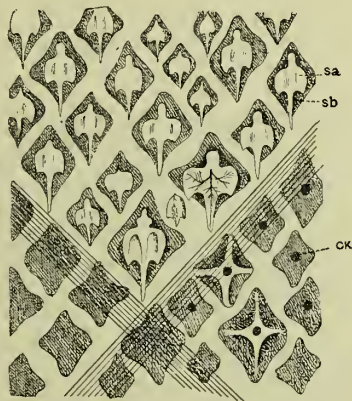


FIG. 65.—Placoid scales of an adult *Scyllium* in surface view (after Klaatsch). The anterior end of the figure is uppermost. The spines are omitted from some of the scales. *Ck* the central canal (pulp cavity) of the spine as it perforates the basal plate *Sb* of the scale; *Sa* spine of the scale.

\* Bles, "Correlated Distribution of Abdominal Pores and Nephrostomes," *Journ. Anat. and Phys.*, 32, 1898, p. 484.

† R. Burckhardt, "Luminous Organs of Selachians, *Ann. and Mag. Nat. Hist.* (7) 6, 1900, p. 558–568.

projects freely on the surface in a backward direction and consists of dentine containing a pulp cavity and capped by enamel. The placoid scales though numerous are not in contact, and fresh scales are continually being developed between them, to replace those worn off. The presence of these spines enables the skin of Plagiostomes to be used by polishers (shagreen). The spines are sometimes much enlarged, e.g. the peculiar spines on male skates, the caudal spine of the sting ray (*Trygon*), the large spines often present on the dorsal fins, etc. The teeth in the mouth are special modifications of placoid scales.

The endoskeleton is entirely cartilaginous, but the cartilage is frequently more or less calcified.

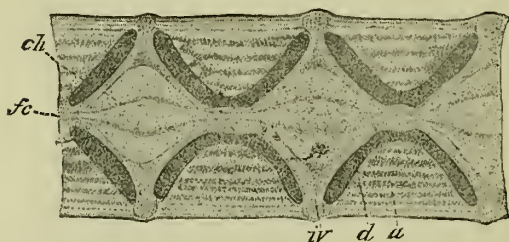


FIG. 66.—Longitudinal section through the vertebral column of *Squatina vulgaris* (after Hasse from Gegenbaur). *a* vertebral body, showing concentric calcified lamellae (cyclospondylos); *iv* intervertebral ligament; *ch* notochord; *fc* attenuated part of notochord. The double calcified cones *d* are shaded dark.

canals. Anatomists are divided on the point, but the preponderance of opinion is in favour of the absence of osseous tissue in Elasmobranchs. Kölliker\* takes this view. Götte† on the other hand holds that the calcified cartilage is true bone. There can be little doubt that bone is quite distinct from cartilage and always arises from elements outside it, possibly as dermal plates. These elements may invade the cartilage and bring about so-called cartilaginous ossification or they may always lie outside it, giving rise to membrane bones proper.‡

The vertebral column § (p. 58) presents the most remarkable

\* Ueb. d. Wirbel der Selachier, *Abh. Senckenb. Ges.* 5.

† *Arch. f. mic. Anat.*, 1878.

‡ Stephan, *Bull. Sci. France et Belgique*, 1900, p. 281.

§ For a detailed account of the vertebral column of Plagiostomes see C. Hasse, *Das natürliche System der Elasmobranchier*, etc., Jena, 1879, 1882 and 1885, and especially A. Kölliker "Über die Beziehung der Chorda zur Bildung der Wirbel der Selachier," etc., *Verhandl. der physik. medic. Gesellsch. zu Würzburg*, 10, 1860, and "Weitere Beobachtungen," etc., *Abhdlg. der Senckenberg. Gesellsch. zu Frankfurt*, 5.

It is possible that perichondrial ossification takes place in some forms in the bodies of the vertebrae between the arches (see p. 124), but the tissue resulting is without cells. This does not however preclude its being bone, for in Teleostei, etc., undoubtedly bone occurs without any bone cells, or haversian



variations which would, in any other group, be regarded as of great morphological importance. It varies in the extent and uniformity of its segmentation, in the arrangement and number of the cartilaginous pieces which enclose the spinal canal, and their mode of attachment to the vertebral central and in the extent of the calcification of the cartilage. It consists typically of a series of amphicoelous vertebrae, through the centra and intervertebral ligaments of which runs the persistent but reduced notochord. The neural arches of each vertebra always consist of more than one piece of cartilage on each side; and the haemal arches extend outwards in the trunk region where they carry short ribs, and downwards, meeting each other ventrally below the caudal artery and vein, in the caudal region. The vertebral column is formed of hyaline and fibro-cartilage, which tissues pass into one another quite gradually.

A tough fibrous membrane, containing cells and surrounded by the elastica externa, is formed (see p. 58) at a comparatively early stage, round the notochord and is called the chordal sheath (Fig. 33). This in most Plagiostomes becomes differentiated into alternately short fibrous and longer cartilaginous portions, i.e. segmented (Fig. 66). The fibrous portions become the intervertebral ligaments, while the cartilaginous portions form the bodies or centra of the vertebrae; so that the vertebrae are described as being *chordo-centrous*. The centra are, however, frequently reinforced by the arch tissue in the manner described on p. 59.

The cartilaginous arches (neural and haemal), which appear in the neural and haemal ridges of the skeletogenous tissue, may, as stated above, spread out round the notochord outside the elastica externa (which may persist or disappear) and unite with each other and so reinforce the vertebral centra; or they may remain separate from one another. In the latter case the neural and haemal arches are separate from the centra; in the former they are continuous with the centra. Kölliker states that in some cases the centra are reinforced by calcified fibro-cartilage which proceeds from the perichondrium of the centra between the insertion of the neural and haemal arches (*Carchariidae*, etc.). In this case we get the cruciform figure in section described below.

In *Chlamydoselachus*, *Echinorhinus*, *Hexanchus* and *Heptanchus*, the cartilaginous notochordal sheath is not definitely segmented: it consists of continuous cartilage, though in the centre

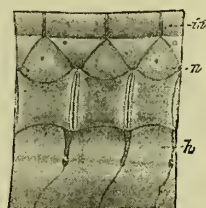


FIG. 67.—Three posterior trunk vertebrae of *Centrophorus* (after Hasse from Gegenbaur). *n* neural arch, with foramen for anterior root; *in* intercalated piece with foramen for posterior root; *h* haemal arch.



of the vertebral regions (as shown by the arches) it has thickened, become firmer, and has encroached upon the notochord (Fig. 68). (In *Chlamydoselachus* this only happens in front, the notochord is unconstricted behind, and in *Heptanchus* the chordal sheath has segmented in the caudal region.)

In other Plagiostomes the notochordal sheath is segmented into alternately cartilaginous portions which constitute the bodies of the vertebrae and fibrous parts which are the intervertebral ligaments (Fig. 66). The sheath thickens in the centre of the vertebral portions and constricts the notochord; moreover its tissue consists of three layers, forming the inner, middle and outer zones. The middle zone is fibrous and is nearly always calcified, forming the so-called double calcareous cone (Fig. 66, c).

In *Hexanchus* and *Laemargus borealis* the vertebrae are entirely uncalcified.

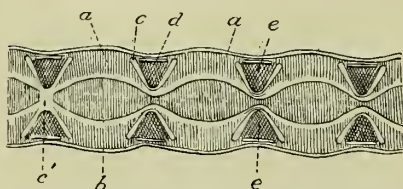


FIG. 68.—Longitudinal section through the hinder part of the vertebral column of *Heptanchus*, showing incipient vertebral bodies (e), and extensive intervertebral ligaments (a), a fibro-cartilage of chorda-sheath; b notochord; c calcified double cone; d external calcification; e hyaline cartilage of the incipient centrum external to the double cone (after Kölliker).

Centra (Fig. 69) in which the internal calcareous matter is confined to the middle zone (double cone) have been called *cyclospondylous*. In some, however, there are additional concentric calcareous rings outside the double cone; such vertebral centra are called *tectospondylous*.

In others again there are radiating calcareous lamellae proceeding from the double cone through the outer zone of the chordal cartilage. Such are termed *asterospondylous*.

The amount of calcification varies from the cyclospondylous condition of the simple double cone with soft tissue outside and inside, to the condition found in many Raji and in the Lamnidæ in which the whole of the chordal sheath is calcified both inside and outside the double cone. The first calcification is always in the chordal sheath in the fibrous tissue of the middle zone (double cone). Later arise the concentric rings of the Tectospondyli or the radiating lamellae of the Asterospondyli; these are calcifications of the hyaline cartilage of the chordal sheath. When skeletogenous tissue is developed outside the *elastica externa* either by an extension of the cartilage of the arches over the centra (many *Cyclospondyli*), or (*Carchariidae*, etc.) by development on the inside of the perichondrium of the centrum, it frequently becomes calcified as four wedges, which extend a certain distance into the body between the insertion of the arches. These hard wedges may or may not reach the double cone (sometimes they do so at the end and not at the centre of a vertebral body); they give rise to the cruciform radiating figure seen in the section of some vertebrae. In such cases the uncalcified cartilaginous arches appear to be continued like

wedges into the centrum. These calcified wedges are formed in a fibrous cartilage or fibrous tissue and contain blood vessels. Calcifications are sometimes found on the surface of the arches or even in their tissue.

It is often difficult to determine in any given vertebra whether the arches grow round and reinforce the centrum unless the *elastica externa* persists, and there seems to be considerable variation in this respect in different animals and even in different parts of the vertebral column of the same animal. In *Hexanchus*, *Heptanchus* (anterior), *Myliobatis* (posterior part), *Rhinobatus* (posterior part), *Trygon* and *Squatina* the arches remain separate and do not grow round the chordal sheath. In *Heptanchus* (posterior), *Centrophorus*, some *Spinacidae* and *Scymnidae*, *Squatina*, many *Rajidae* the arches grow round and reinforce the centrum. In the *Carchariidae* and *Lamnidae* the centrum is strongly reinforced by perichondrial calcification and the cruciform appearance in section is very marked, but it is not clear whether the arches contribute to the centrum.

The neural and haemal arches are always segmented. The neural arch is generally incomplete, being supplemented by the intercalated pieces (Fig. 67), and there are often some special supra-dorsal pieces which form the actual roof. In some cases (*Alopias*) both neural

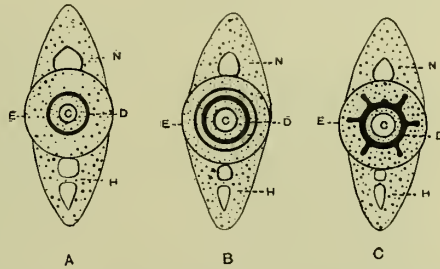


FIG. 69.—Diagrammatic transverse sections of vertebrae, to illustrate *A* the cyclospondylous; *B* the tectospondylous; and *C* the asterospondylous condition. *C* notochord; *D* central calcareous ring; *E* elastic externa; *N* neural, *H* haemal arch (from Hasse).

arches and intercalated pieces extend across the roof of the spinal canal (Fig. 70). The anterior root of a spinal nerve frequently perforates the neural arch, the posterior root the intercalated piece, or the nerves may pass out between the arch and the intercalated piece. In the trunk region the vertebrae carry short dorsal spinous processes, but in the caudal region these may attain some length. There is a longitudinal elastic ligament extending along the ridge of the upper arches; it may be embedded in the cartilage.

Sometimes (Fig. 71) more than one pair of intercalated pieces may occur in each vertebra, and the number may vary in different parts of the vertebral column of the same animal. In *Zygaena* there are two. It frequently happens that in the caudal region there are two complete vertebrae (centrum, arch, intercalated pieces, etc.) for every spinal nerve (diplospondyly).\*

\* W. Ridewood, "Caudal diplospondyly of Sharks," *Journ. Linn. Soc.*, 27.

In the middle part of the trunk region in the *Notidanidae*, each centrum carries two sets of neural arches and intercalated pieces, and corresponds to two pairs of spinal nerves, and therefore to two segments.

The haemal arches, which are sometimes supplemented by intercalated pieces, are in the trunk directed outwards, and carry very short ribs; in the tail they are directed ventralwards, and meet below the caudal artery and vein.

In the Raji the anterior vertebrae are not separate, but form a continuous cartilaginous structure into which the notochord extends only for a short distance and which articulates with the occipital region of the skull. In *Notidanidae* the anterior part of vertebral column has fused to the skull.

The cranium, of which a general description is given on p. 60, consists of continuous cartilage, which may be partially calcified.

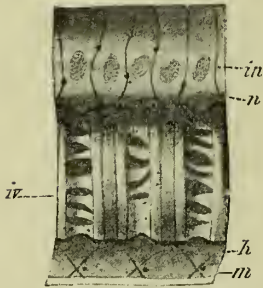


FIG. 70.—Three trunk vertebrae of *Alopias vulpes* (from Gegenbaur, after Hasse). *iv* intervertebral ligament; *n* neural arch; *in* intercalated piece of neural arch, *m* of haemal arch (*h*).

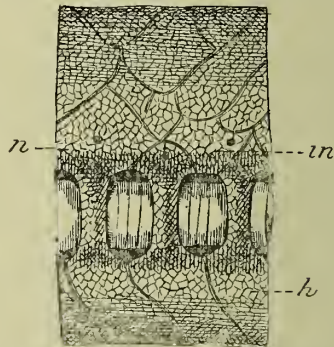


FIG. 71.—Lateral view of a portion of the caudal vertebral column of *Rhinoptera* (*Zygobates*) (after Hasse), showing large number of extra dorsal pieces above the intercalated pieces *in* and the neural arches *n*. The neural arches are continued into the haemal *h* round the centra.

The notochord may be entirely atrophied in the parachordal region (Raji, etc.) or it may persist to a greater or less extent (*Heptanchus*, *Centrophorus*, *Acanthias*, *Squatina*, *Prionodon*). In Raji there is a distinct articulation between the occipital region and the anterior vertebral plate of the vertebral column by means of two occipital condyles and an 'odontoid process' of the vertebral plate. In the Squali there are also usually two occipital condyles, but no regular joint between the first vertebra and the skull. In the *Notidanidae*, in which the anterior end of the notochordal sheath is not segmented, the latter structure runs continuously into the cartilaginous region of the skull.

The occipital region is more sharply marked off from the vertebral column in the Raji than in the Squali. In correspondence with this the occipito-spinal nerves (p. 138) are reduced or absent in Raji. In a few cases the occipital cartilage extends back over the anterior vertebrae and envelopes them (*Carcharias*), while in *Mustelus* one vertebra is fused with the skull.

The greater part of the roof of the skull is formed of cartilage, but there is a well-marked median fontanelle in the roof of the ethmoidal region. The space in the auditory cartilage in which the otocyst lies communicates with a canal which contains the aqueductus vestibuli and opens on the dorsal surface, either into a depression in the cartilage which receives the opening of the

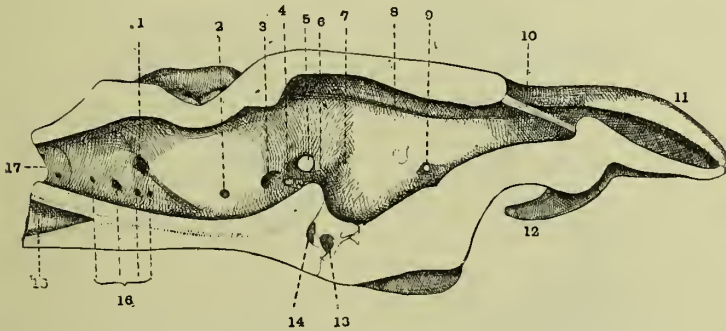


FIG. 72.—Median section of the cranium of *Hezanchus*, inner view (after Gegenbaur). Foramen for 1 vagus, 2 glossopharyngeal, 3 auditory, 4 facial, 5 trigeminal nerve; 6 posterior clinoid ridge; foramen for 7 oculomotor, 8 trochlear, 9 optic nerve; 10 fontanelle; 11 rostrum; 12 lateral process of ethmoid region; 13 foramen for carotid; 14 transverse canal in skull base; 15 notochord; 16 foramina for spino-occipital nerves; 17 neural arch of the first vertebra with nerve foramina.

corresponding canal of the other side (*Squali*) or on the surface separately from the latter (*Raji*).

The ethmoidal region is frequently prolonged in front of the nasal capsules. In the *Raji* and a few *Squali* this continuation is a well-marked process, the *rostrum* (very largely developed in *Pristis*); in *Squali* it is, if present, usually confined to a slender process, the prenasal process, with which two processes of the nasal capsules may be connected.

The labial cartilages are small cartilaginous rods in folds of skin at the sides of the mouth, near the angle; there are usually two pairs above and one pair below. They are less developed and less constant in the *Raji*.

**Visceral Arches** (p. 61).—The mandibular arch is always



divided into two pieces ; of these the dorsal forms the skeleton of the upper jaw, and is called the palato-quadrate bar, while the ventral constitutes the lower jaw and is called the cartilage of Meckel. The dorsal posterior end of Meckel's cartilage articulates with the hind and ventral end (quadrate portion) of the palato-quadrate bar, while the ventral anterior end meets its fellow at the symphysis of the lower jaw. Anteriorly the palato-quadrate bar joins its fellow beneath the ethmoid region but its relation to the skull varies in the most remarkable manner throughout

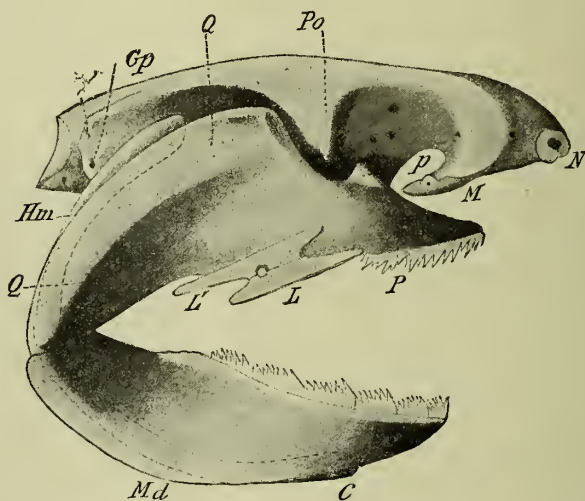


FIG. 73.—Skull of *Hexanchus* with mandibular and hyoid arch (after Gegenbaur). P-Q palato-quadrate; Hm hyomandibular; Md Meckel's cartilage; C basihyal, L, L' labial cartilages; p palatine process of palato-quadrate; M lateral process of ethmoid; N nasal sac; Po postorbital process; Gp foramen for glossopharyngeal nerve.

the group. In the *Notidanidae* (Fig. 73) it articulates with the skull at two points ; anteriorly it has a process, the palatine process, which is connected with the skull between the exit of the optic and trigeminal nerves, while posteriorly it articulates with the postorbital process of the auditory cartilage, *i.e.* anterior to the spiracle. In these skulls the hyoid arch, which bears branchial rays, is attached to the auditory region and is segmented into two pieces on each side and a median piece, the hypohyal or copula.

In other Selachians the palatine process is present, though the



connection is further forwards with the ethmoid region (ethmo-palatine ligament), but the posterior articulation, viz. with the postorbital process is not present. On the other hand the posterior end of the bar is attached to the dorsal element of the hyoid arch by ligaments.

In such Selachii the condition of the hyoid is very similar to that in the *Notidanidae* (already described), excepting that the dorsal piece is much stouter and assists to a marked extent by means of ligamentous bands, attaching it to both the quadrate end of the palato-quadrate bar and to Meckel's cartilage, in supporting the mandibular arch. This dorsal piece is for this reason called the hyomandibular, the other piece being called the ceratohyal. In *Raji* the palatoquadrate bar is without

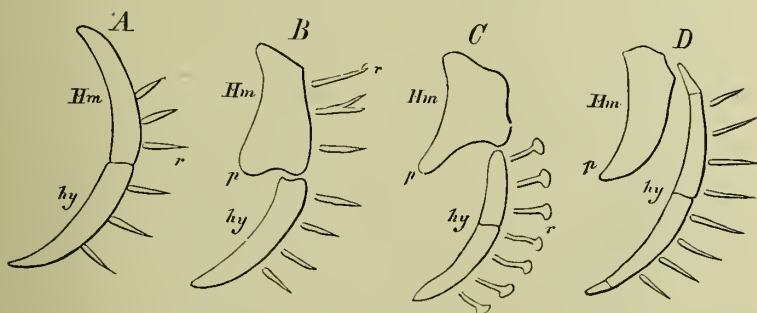


FIG. 74.—Diagram showing the principal modifications in the arrangement of the hyoid arch in Plagiostomes (after Gegenbaur). *A* in *Notidanus*; *B* in pentanchal Selachians; *C* in *Torpedo*; *D* in *Raja*. *Hm* hyomandibular; *p* process of *Hm*; *hy* lower part of hyoid arch; *r* branchial rays.

the palatine process, and the mandibular arch is entirely supported by the hyomandibular. This structure is without gill-rays and has developed a process for the support of the mandibular arch (Fig. 74, *p*). It has almost lost its relation to the lower part of the hyoid arch, which is connected only to its dorsal end, or is attached dorsally direct to the auditory cartilage (many *Rajidae*, etc.). The hyoid arch of such forms is only equivalent to the ventral part of the hyoid of the *Notidanidae* and *Squali* generally. It is a comparatively slender, jointed structure, closely resembling the posterior branchial arches, like which it bears branchial rays. There are frequently two or three small cartilages, the *prespiracular* cartilages, in the anterior wall of the spiracle.

In the *Holocephali* the autostylic arrangement (p. 63) prevails, the palato-quadrate bar being continuous with the skull.

The branchial arches are typically and usually segmented into four pieces on each side and a median piece, the basibranchial or copula. The dorsal of the four pieces is called the pharyngobranchial, the second the epibranchial, the third the ceratobranchial, while the ventral and smallest piece is called the hypobranchial.

The hypo- and basi-branchial pieces are somewhat variable, the hypobranchial of the anterior arches being often undeveloped (some Raji) and the basibranchial being often absent from the anterior arches. In the latter case the last basibranchial (cardiobranchial) which is always larger than the others, is much developed and has several arches attached to it. The hypobranchial of the first arch is frequently attached to the basihyal. The last arch is always smaller than the others; its pharyngobranchial is fused with the pharyngobranchial of the preceding arch and its hypobranchial is not developed. In Raji the last arch articulates with the shoulder girdle. In Squali the dorsal elements are not closely attached to the vertebral column, but in Raji there is a firm attachment. All the branchial arches except the last bear branchial rays on the epi- and ceratobranchial segments; and in most Squali cartilaginous rods called extra-branchials are placed close beneath the skin near some of the external branchial apertures; they are absent in Raji.

The supporting structures of the median fins are, as in the case of the paired fins, of two kinds; the cartilaginous somactids and the horny dermatrichia. In the dorsal fins, in the dorsal part of the caudal, and in the anal fin the dermatrichia are carried by somactids which are usually imbedded in the muscles and not attached to the neural or haemal spines. In the ventral lobe of the caudal fin there are no somactids and the dermatrichia are carried by the haemal spines.

The pectoral girdle consists of two dorso-ventrally directed cartilaginous rods, placed one on each side of the body, and each divided by the surface (*glenoid*) for the articulation of the skeleton of the pectoral fin into a dorsal portion, the *scapula*, and a ventral portion, the *coracoid*. The two coracoids are continuous with one another ventrally, beneath the pericardium, but the scapulas end freely dorsally, except in Raji, in which the dorsal portion, sometimes partly marked off as a supra-scapula, is attached to the anterior vertebral plate (p. 126) of the spinal column.

The skeleton of the pectoral fin consists of a number of

somactids, which carry peripherally the dermatrichia.\* There are generally three basal somactids which articulate directly with the pectoral girdle (Fig. 75, *B*): these are called respectively the pro- meso- and meta-pterygium. They carry the peripheral radialia. The metapterygium is the largest of the basal pieces and carries the greatest number of peripheral somactids. These are placed mainly on its preaxial side (Fig. 75), there being few, if any, on its postaxial side.

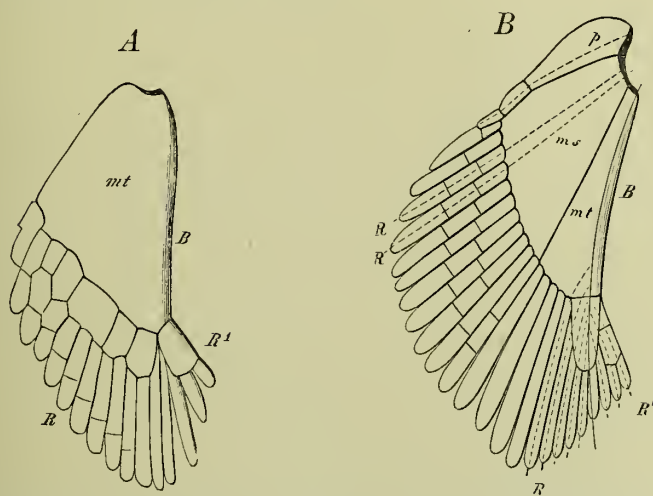


Fig. 75.—Skeleton of pectoral fin *A* of *Scymnus*, *B* of *Acanthias vulgaris* (after Gegenbaur). *p* pro-, *ms* meso-, *mt* meta-pterygium; *B* postaxial (median) side of fin. (The line drawn through *mt* in *B* indicates what some anatomists regard as the axis of the so-called archipterygium; on the same view the dotted lines *R*, *R* indicate the preaxial radii, *R'* the postaxial radii).

The metapterygium appears to be the most important basal, and when there is only one basal somactid, as in *Scymnus* (Fig. 75, *A*), it is supposed to be the metapterygium.

In living forms the fin-skeleton is always rhipidostichous (p. 57), but in some extinct forms (*Cladoselache*, Fig. 83) it is orthostichous, and in others (*Pleuracanthus*, Fig. 76) it is rachiostichous (and unibasal) and on the whole pleurorachic (p. 57). In Raji the propterygium and mesopterygium are elongated and segmented, and the propterygium is attached to the olfactory region of the skull. Moreover in the Raji there are sometimes additional basals inserted between the meso- and meta-pterygium.

The pelvic girdle is not attached to the vertebral column; it consists of a transverse bar of cartilage placed just ventral to

\* Dermatrichia are absent from the paired fins of some Raji (e.g. *Torpedo*, etc.).

the cloaca and carrying at its outer end the skeleton of the fin. The main portion may be called the ischio-pubic portion, the short process external and anterior to the limb being all that can be compared to an ilium.

The fin presents two basal cartilages of which the larger is the metapterygium and carries most of the peripheral somatids; the propterygium is small. In the male the metapterygium is continued to form the skeleton of the clasper.

Here as in the fore-limb there is some variation in the number of basal cartilages, mainly manifested in extinct forms.

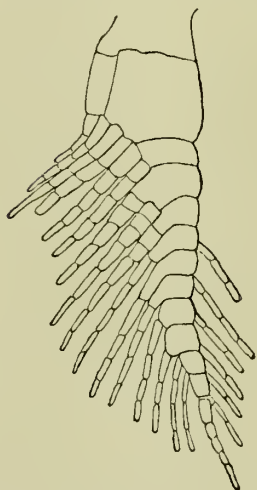


FIG. 76.—Skeleton of right pectoral fin of *Pleuracanthus* (*Xenacanthus*) *decheni* (after A. Fritsch, from Gegenbaur).

The **brain** \* (Figs. 77, 78) of Plagiostomes presents great variations but is always characterised by the following features: (1) The olfactory lobes, which may be placed some distance in front of the cerebrum and connected with the latter by a long stalk, or may be placed quite close to the cerebrum, are connected with the cerebrum laterally and somewhat dorsally; (2) the cerebrum is unpaired though internally it possesses two lateral ventricles, each of which is usually continued into its olfactory lobe; it is not sharply marked off from the thalamencephalon; (3) the epiphysis is elongated, its front end lying over the cerebrum either beneath or just behind the cranial fontanelle (in *Raja* in the subcutaneous tissue above the fontanelle); (4) the optic nerves form a chiasma, and the infundibulum has lobi inferiores and an infundibular gland (*saccus vasculosus*); (5) the cerebellum is large and its surface is frequently convoluted. There is said to be a paraphysis, but there is

\* N. v. Miklucho-Maclay, *Beiträge zur vergl. Neurologie d. Wirbelthiere*, Leipzig, 1870. J. V. Rohon, "Das Centralorgan des Nervensystems der Selachier," *Denkschr. d. Wiener Akad. Math., etc.*, 38, 1877. L. Etinger, "Unters. üb. d. vergl. Anat. des Gehirns, *Abh. d. Senckenbergischen naturf. Gesellschaft*, i. and ii. 1888 and 1892.

no pineal eye (parietal organ). The pituitary body lies along the ventral side of the infundibulum; it is said to open in the adult into the cranial cavity within the dura mater (Haller), but this must be regarded as doubtful.

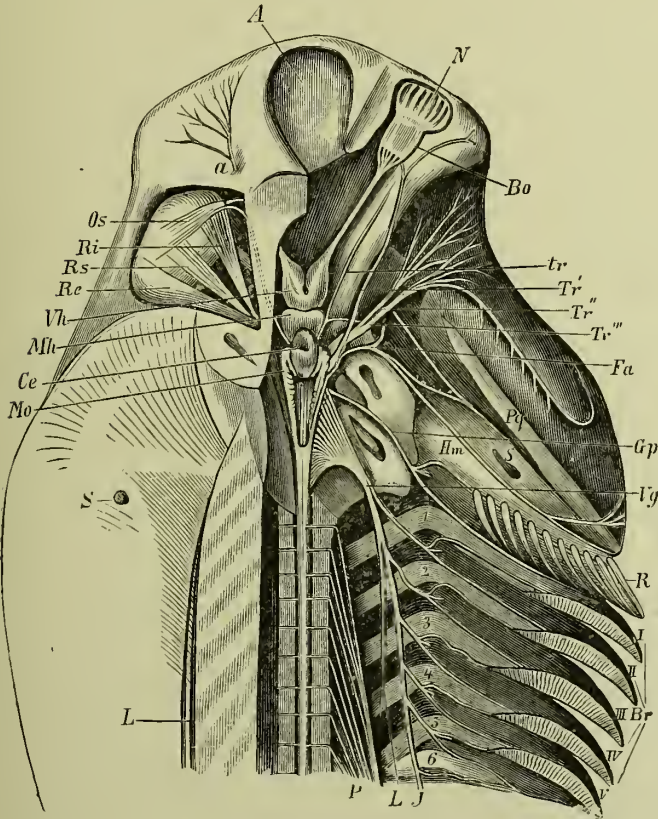


FIG. 77.—Brain and anterior part of the spinal cord and nerves of *Hexanchus griseus* (after Gegenbaur, from Claus). The nerves are exposed on the right side, and the right eye is removed. *a* terminal branches of ophthalmicus superficialis trigemini; *Bo* olfactory lobe; *Br* branchiae; *Ce* cerebellum; *Fa* seventh nerve (facial); *Hm* hyomandibular; *Gp* ninth nerve (glossopharyngeal); *J* intestinal branch of vagus; *L* lateralis of vagus nerve; *Mh* optic lobes (mid brain); *Mo* medulla oblongata; *N* nasal capsule; *Os* superior oblique muscle of eye; *P* spinal nerves; *Pq* palatoquadrate; *R* branchial rays; *Re* external, *Ri* internal, *Rs* superior rectus muscle of eye; *S* spiracle; *tr* fourth nerve (trochlear); *Tr'* ophthalmicus superficialis trigemini; *Tr''* superior, *Tr'''* interior maxillary branch of the fifth nerve; *Vg* tenth nerve (vagus); *Vh* cerebrum (forebrain); 1-6 branchial arches.

The cerebrum is generally marked by longitudinal grooves indicating the internal division, but in *Carcharias* (Fig. 78), *Sphyrna*, etc., there are no traces of these. Plagiostomes



differ considerably as to the length of the thalamencephalon.\* In some, this part of the brain is much elongated, being completely exposed in its dorsal part and passing without break into the anteriorly-placed cerebrum (*Notidanidae*, *Spinacidae*, *Scymnidae* and most Plagiostomes). In others the thalamencephalon is very short and its dorsal surface is almost completely covered by the cerebrum, the hinder part of which almost, if not quite, touches the optic lobes (*Carcharias*, *Sphyrna*, *Oxyrrhina*, *Galeus*, *Trygon*). It would appear that the latter condition is developmentally the most primitive, for brains with a long thalamencephalon in the adult, e.g. *Scyllium*, have in the later embryonic stages a short thalamencephalon with the cerebrum and optic lobes in contact over it.

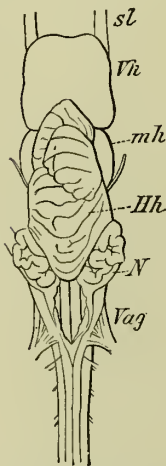


FIG. 78.—Brain of *Carcharias* from above (after Miklucho-Maclay). *sl* olfactory lobe; *Vh* cerebrum; *mh* optic lobe; *Hh* cerebellum; *N* restiform tract; *Vag* vagus.

The cerebellum in some forms is very large and may reach forward to the cerebrum. The restiform tracts, or sides of the medulla are much developed, and folded or even convoluted. This is ascribed by Burckhardt to the enormous development of the sensorial centres in the dorso-lateral parts of the spinal cord and brain in consequence of the insertion of the nerves of the lateral line organs.

The dorso-median tract of non-nervous tissue which is so often found along the central nervous system of the Vertebrata and was first mentioned by the physiologist Haller (*Opera Minora*, 1768, bd. 3) has been detected as a septum in the cerebellum of many Plagiostomes. It is of course also present, as in all Vertebrates, over the third and fourth ventricles and on the posterior wall of the lateral ventricle. Very possibly the very thin dorsal wall—at the bottom of the dorsal fissure—of the central canal of the spinal cord is to be regarded as part of it, though there is here a little nervous tissue.

**Cranial nerves** † (see p. 72). There is nothing special to

\* This and other features of the brain seem to be influenced by the size and position of the eyes, vide Burckhardt, *British Association Reports*, 1900.

† H. Stannius, *Das peripherische Nervensystem der Fische*, Rostock, 1849. J. C. Ewart, "On the Cranial Nerves of Elasmobranch Fishes," *Proc. Roy. Soc.*, 45, 1889, p. 524. Id., *Supplementary note on the cranial nerves of Elasmobranchs*, Edinburgh, 1892. A. M. Marshall and W. B. Spencer, "On

note about the first, second, third, fourth, and sixth cranial nerves.

The ophthalmicus profundus (Fig. 79, *opv*) is a well marked and distinct nerve in most Elasmobranchs, but in some (e.g. *Scyllium*) it is less marked. It arises either with or just in front of (*Laemargus*) the main root of the trigeminal. After emerging from the skull wall with the trigeminal it presents a ganglion—the *profundus ganglion*, and passes forwards in the orbit, dorsal to the external and internal recti, but ventral to the superior rectus and superior oblique. It penetrates the anterior wall of the orbit, and is distributed to the skin of the front of the snout. In the orbit it gives off long ciliary nerves to the eyeball, and one or more nerves which anastomose with one or more filaments from the ventral branch of the oculomotor (*om*), a small ganglionic swelling being found at the point of junction. This small ganglion is the ciliary or oculo-motor (lenticular, ophthalmic) ganglion; it gives off some ciliary nerves (short ciliary) to the eyeball. The filaments connecting this ciliary ganglion with the ophthalmicus profundus (sometimes with the profundus ganglion) constitute the *radix longa*, while those passing to the oculomotor represent the *radix brevis*. The filaments passing from the ciliary ganglion to the eyeball represent the short ciliary nerves.

The ciliary ganglion of Plagiostomes seems to be variable in its size and position; it is sometimes absent, sometimes close to the profundus nerve, sometimes approximated to the ventral branch of the third nerve. In the embryo the oculomotor nerve passes directly from its origin to the profundus ganglion; later it becomes detached, the connecting cord being the *radix brevis*. The ciliary ganglion is probably a detached portion of the profundus ganglion, in which case its relation to this ganglion is exactly that of a sympathetic ganglion to the ganglion of a posterior root of a spinal nerve. The ophthalmicus profundus itself probably corresponds to the nasal nerve of the *Mammalia*. The third nerve must be regarded as the ventral root of a nerve of which the ophthalmicus profundus is the dorsal (see p. 73).

The trigeminal nerve arises usually by a single root from the sides of the medulla. It swells either inside or outside the cranium into the gasserian ganglion and there gives off the

the cranial nerves of *Scyllium*," *Q. J. M. S.*, 21, 1881, p. 469. C. Gegenbaur, "Die Kopfnerven von *Hexanchus*," *Jena. Zeitsch.*, 6, 1871, p. 497. F. J. Cole, "On the cranial nerves of *Chimaera*," *Trans. Roy. Soc. of Edinburgh*, 38, 1896, p. 631. Also literature cited on p. 75.

superficial ophthalmic (*ramus ophthalmicus superficialis, sot*). This nerve, which is quite inconspicuous in Raji and in forms in which the ophthalmicus profundus is well developed (at once joining the ophthalmic branch of the facial), runs close to or in conjunction with the superficial ophthalmic of the facial; it is distributed to the subcutaneous tissue and skin of the snout. The main nerve passes on and divides into the superior and inferior maxillary branches. Of these the inferior maxillary is a mixed nerve; the superior being mainly sensory but containing motor fibres in some forms (e.g. *Chimaera*).

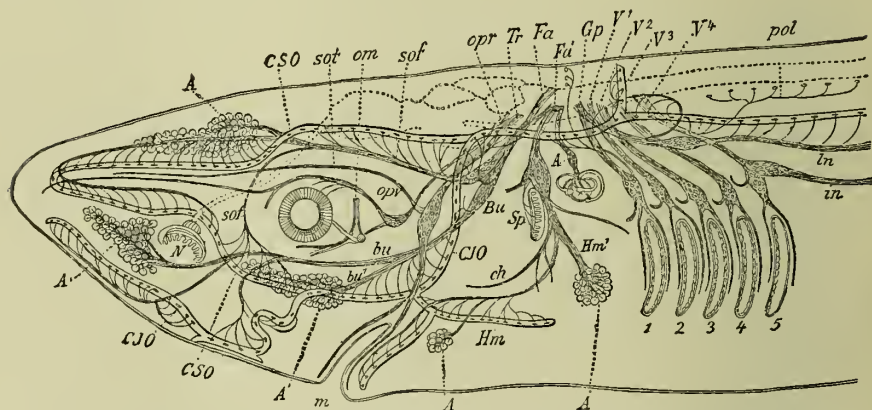


FIG. 79.—Diagram illustrating the distribution of the dorsal branches of the cranial nerves of the lateral line canals, and the position of the groups of ampullae in an Elasmobranch (after Ewart, from Gegenbaur). *A* auditory nerve with labyrinth; it also points to the groups of Lorenzini's ampullae; *Bu* buccal branch of facial, *bu* inner branch to part of infraorbital canal, and to the inner buccal group of ampullae; *bu'* its outer branch which supplies the part of the infraorbital canal, and the outer buccal group of ampullae; *ch* postbranchial branch of facial to mucous membrane, and giving off motor branches to some jaw muscles; *CSO*, *CSO* supraorbital canal; *CJO*, *CJO* infraorbital canal; *Fa*, *Fa'* roots of facial nerve; *Gp* glossopharyngeal, arising under cover of the lateral branch of the vagus nerve; *Hm* hyomandibular canal arising from the infraorbital and giving off the mandibular canal; the mandibular group of ampullae is in the angle between these two; *Hm'* branch of the hyomandibular nerve to the hyoid group of ampullae; *in* lateralis branch of vagus with ganglion, where it separates from fourth branchial branch; *ln* lateralis branch of vagus nerve; *m* mouth; *N* nasal sac; *om* deep branch of oculomotor giving off short root of ciliary ganglion (shown, but not marked), the long root is also shown, as are the short ciliary nerves to the eye; *opr* root of ophthalmicus profundus; *opt* dorsal branch of same, giving off long ciliary nerves; *pol* second branch of lateralis supplying some lateral line sense organs, and a row of pit organs, the first branch supplies the commissure connecting the two lateral canals, and some sense organs of the main canal; *sof* ophthalmicus superficialis facialis, which supplies the supraorbital canal, and the superficial ophthalmic group of ampullae; *sot* ophthalmicus superficialis trigemini; it arises from the gasserian ganglion; *sp* spiracle; *Tr* trigemini; *V<sup>1</sup>*, *V<sup>2</sup>*, *V<sup>3</sup>* the first three branchial branches of the vagus nerve, each with a ganglion and with pharyngeal, prebranchial and postbranchial branches; *V<sup>4</sup>* the united fourth branchial branch of vagus and intestinal branch; 1-5 gill-slits.

The facial nerve with its ganglion, the geniculate ganglion, has three or four roots which after communicating with one another separate into three nerves, the *ophthalmicus superficialis*

*portio facialis* (*sof*), the *buccal* (*Bu*), and the *hyomandibular* nerves (*Fa'*, *ch*, *Hm'*). The two first of these and the external mandibular branch of the last innervate the sense organs of the sensory tubes. The hyomandibular \* excluding the external mandibular branch may be called the facial proper (*ch*) ; it is a mixed nerve for the hyoid arch with branches to the roof of the mouth (*palatine*) and mandibular arch (*prespiracular*).

The three roots of the facial are as follows: a dorsal root (*Fa*), from which probably most of the lateral-sense organ nerves are derived, and two ventral roots, of which the anterior is just behind the root of the 5th and is possibly double, while the posterior is just in front of the root of the auditory.

The ophthalmicus superficialis freely communicates with the buccal nerve as it passes through the cranial wall which it does by a foramen dorsal to that for the trigeminal. Outside the cranium it presents a ganglion and passing along the dorsal side of the orbit is distributed to the supraorbital branch of the cephalic lateral line and to the ampullae of the ampullary canals of the snout.

The buccal nerve (*bu*, *bu'*) after passing through the cranial wall with the trigeminus becomes closely applied to the gas-serian ganglion and swells into a ganglion. It runs along the floor of the orbit close to the maxillary nerve. It supplies the inner and outer buccal groups of ampullae, and the sense organs of the orbital and suborbital lateral line.

The hyomandibular nerve, after leaving the skull by a foramen which is generally through the auditory cartilage, behind and distinct from the trigeminal, dilates into a ganglion where it gives off forward the palatine nerve (indicated but not marked in the figure). The palatine nerve at once gives off the prespiracular nerves which are supposed to be homologous with the chorda tympani of mammals, and is continued to supply the roof of the mouth. It is homologised with the great superficial petrosal of mammals. The hyomandibular then gives off a branch to the mandibular and hyoid group of ampullae and lateral line—the external mandibular—and is continued to the muscles, etc., of the hyoid arch (internal mandibular of Stannius, *ch*).

The auditory nerve arises by a root immediately behind

\* In the figure the hyomandibular nerve (*ch*) is smaller than the external mandibular which runs with it, so that it appears as a branch of the latter.



those of the trigemino-facial group and is distributed to the walls of the otocyst.

The glossopharyngeal (*Gp*) arises just in front of the vagus by three or four rootlets. It passes out by a canal below the auditory capsule, dilates into a ganglion and gives off a small dorsal nerve which in some cases is said to supply a part of the cephalic lateral line. The nerve continues to the first branchial arch giving off a prebranchial branch to the hyoid and a pharyngeal branch.

In the vagus the root of the lateral line nerve (*lateralis*) must be distinguished from the roots of the rest of the nerve. The *lateralis* nerve (*ln*) arises by a root dorsal to and slightly in front of the glossopharyngeal. It leaves the skull with the rest of the vagus to which it is closely applied and dilates into a ganglion. It is continued to the end of the body and supplies the trunk portion of the lateral line canal, and a small portion of the cranial lateral line. The remaining vagus roots, which are numerous, unite to form five nerves each of which has a ganglion. These are at first closely connected together and are distributed in the typical manner, the first four to the four hinder branchial arches and the last is continued as the intestinal branch (*in*).

A variable number of anterior roots of spinal nerves \* of which the posterior roots though present in the embryo are absent in the adult, arise from the medulla ventral to the vagus roots. They were formerly mistaken by Gegenbaur for ventral roots of the vagus and were called ventral vagus roots. They are absent in some Raji. They leave the skull wall by special foramina in the occipital region and innervate some muscles of the fore-limb and some ventral branchial muscles. They are called the *spino-occipital* nerves.

It has been shown in Amphibia that the superficial ophthalmic of the facial, the buccal and external mandibular of the facial and the *lateralis* of the vagus arise from the acustico-lateralis nucleus in the brain (see p. 75). All these nerves are developed from the surface ectoderm and sink inwards to their adult positions and when in Amphibia the lateral line sense organs disappear the whole of these nerves disappear also.

\* M. Fürbringer, *Ueb. d. Spino-occipitalen Nerven der Selachier, etc.*, Leipzig, 1897.



In *Chimaera* a small portion of the supraorbital canal is supplied by the ophthalmicus profundus, and in some if not all Plagiostomes (*Mustelus*, *Laemargus*), Teleosts, Ganoids, the dorsal branch of the glosso-pharyngeal innervates a small portion of the cephalic lateral line.

For an account of the **sense organs** the reader is referred to p. 121, and to the section dealing with Pisces (pp. 77-82). For the **sympathetic**, see p. 75.

The **alimentary canal** is fairly similar throughout the order. The mouth is usually ventral. Teeth varying considerably in shape are present in several rows on the palato-quadrate bar and cartilage of Meckel. As those in the row next the mouth opening are worn away, those of the next row advance, and a new row is added internally. The basihyal projects in a tongue-like manner from the floor of the mouth. There are no salivary glands. The hinder part of the mouth passes without demarcation into the pharynx which receives the internal openings of the spiracle and gill-slits.

The oesophagus leads into the stomach, which is **U**-shaped, the pyloric limb of the **U** being narrow and opening into the short somewhat swollen anterior end of the intestine (duodenum, *bursarentiana*). Into this open the bile duct and the pancreatic duct. It is followed by the rest of the intestine which is provided with a spirally disposed longitudinal valve. The intestine ends behind in a narrow rectum, which receives a dorsal gland, the rectal gland, and opens into the cloaca. The cloaca opens externally between the pelvic fins. The alimentary canal is supported by a mesentery which is defective in part. The liver is well developed and usually provided with a gall bladder. The pancreas is also large. There is a well-developed spleen in the neighbourhood of the stomach.

In *Laemargus borealis* two large caeca open into the commencement of the intestine. In some forms (*Zygaena*, *Carcharias*) the longitudinal valve is not spirally arranged, but is rolled upon itself.

There is no **air-bladder**.

A **thyroid** is present between the rami of the mandibles. It frequently has a pyriform shape and lies over the bifurcation of the ventral aorta.

The **thymus** is represented by an elongated lobed gland placed over the dorsal ends of the branchial arches and derived, as usual,

from epithelial outgrowths of the embryonic branchial passages.

**Body cavity.** The pericardial cavity communicates with the general body-cavity by a canal which leaves it dorsal to the sinus venosus and passing along the ventral side of the oesophagus opens behind by a slit-like aperture into the body-cavity. This canal may divide in a Y-shaped manner behind, but usually only one of the limbs is complete.

The body-cavity may communicate with the exterior by abdominal pores, with the kidney-tubules by persistent nephrostomes and with the cloaca by the oviducts.

Abdominal pores are usually present, though there is considerable variability as to these openings in closely allied species or even in the same species at different periods of life. They are placed on each side of the cloacal opening, either on the surface or at the bottom of a pouch (cloacal pouch). They lead into that part of the body cavity which is placed on each side of the cloaca (peritoneal canals).

The **vascular system** is arranged in the usual piscine manner. The pericardial cavity is placed dorsal to the median union of the coracoid cartilages of the shoulder girdle. Its walls are stiffened by that skeletal structure and by the basibranchial plate which lies dorsal to it. It thus happens that its walls are unyielding and when the ventricle contracts, blood flows from the great venous sinuses outside the pericardium into the large auricle. The ventricle is provided with a muscular conus arteriosus in which there are from two to five or even more rows of semilunar valves. The ventral aorta sends branches to the hyoid arch, which has a demibranch on its hinder face, and to all the branchial arches except the last. The carotids arise from the dorsal system and the internal carotids anastomose as they enter the cranial cavity. The efferent vessel coming from the hyoid demibranch gives off near its ventral end an artery which passes forward ventrally to the spiracle on to the mandibular arch. It passes near the front wall of the spiracle, giving off vessels to the pseudo branch and then pierces the cranial wall to join the internal carotid artery within the skull.

The great veins are much dilated into sinuses as they approach the heart. This applies to the anterior and posterior cardinals and to the hepatic veins. Moreover the anterior cardinal is dilated round the eye-ball forming the space (a kind of hæmo-

coelic body-cavity) in which the movements of the eye occur. There is a renal-portal system furnished by the caudal vein which branches when it reaches the kidney, and the posterior cardinals arise in the kidney.

The **kidney** (Fig. 81) of each side is a single gland but by the arrangement of the collecting tubules may be divided into an anterior thin part, the mesonephros (almost absent in the adult female), and a posterior thick well-developed portion the metanephros. The longitudinal duct extends along the whole length of the gland and posteriorly joins its fellow to form an unpaired tube—the urinary sinus—which opens into the cloaca. This duct has various names none of which are entirely satisfactory. It is called the pronephric, the mesonephric, and the wolffian duct (p. 89). We shall call it usually the longitudinal duct. The collecting tubes of the mesonephros are directed transversely and open at once into the longitudinal duct; the collecting tubules of the metanephros, the so-called **ureters**, are directed backwards and after a certain amount of union amongst themselves open into the hinder part of the longitudinal duct close to the urinary sinus by one or more openings.

The ovaries and testes are slung to the dorsal wall of the body-cavity by the mesovarium and mesorchium respectively, membranes which are either attached close to the mesentery or to the mesentery itself. In some few cases the ovaries of the two sides are united into one body which is placed slightly on the right side. The testes are connected with the anterior end of the mesonephros by a network of tubules—the testicular network (Fig. 80), which is not visible (Fig. 81) without special preparation, and which typically consists of the longitudinal canal of the testis, the longitudinal canal of the mesonephros (wolffian body) and the vasa efferentia connecting these two. The longitudinal canal of the mesonephros (wolffian body) is connected with the malpighian bodies of a number of the anterior mesonephric tubules. The number of tubules implicated varies very considerably in different species, and very possibly in individuals of the same species. In *Scyllium canicula* it appears frequently to be four, in *Squatina vulgaris* five. The sperm therefore passes through anterior kidney tubules into the longitudinal duct which is in the male much convoluted and functions as the vas deferens. The hind end of the longitudinal duct is dilated to form the vesi-

cula seminalis (Fig. 81, *vs*). The two vesiculæ seminales join to form the urogenital sinus and just before their union each receives the opening of the seminal bladder (*ss*), which is a pouch lying on the ventral side of the vesicula seminalis, and the openings of the ureters, usually four or five in number in *Scyllium canicula*. The urinary sinus which in the male is common to the urinary and generative organs opens into the cloaca through its dorsal wall by a median papilla—the urinogenital papilla (*ug.p.*).

In the female the hind end of the longitudinal duct is dilated (*ub*) and receives not far from its union with its fellow the ureters

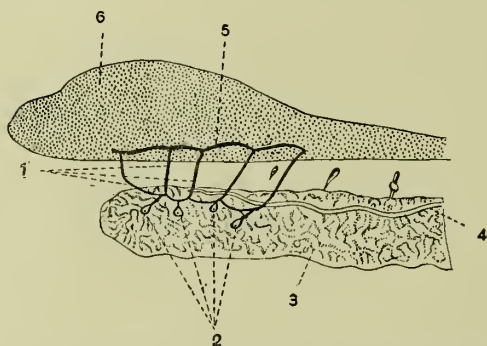


FIG. 80.—Testis and anterior part of mesonephros (Wolffian body) of an embryo of *Squatina vulgaris* (after Balfour): to show the testicular network. There are five vasa efferentia connecting the longitudinal canal in the base of the testis with a longitudinal canal in the mesonephros. From the latter there pass off four ducts to as many malpighian bodies. 1 vasa efferentia; 2 malpighian bodies; 3 mesonephros; 4 longitudinal or mesonephric duct; 5 longitudinal canal of the testis; 6 testis.

(*ur*) by one or more openings. The oviducts open close together through the dorsal wall of the cloaca in front of the urinary papilla. They extend forward to the front end of the body cavity into which they open close together on the ventral side of the

anterior end of the liver (*fl.t'*). Not far from their front end their walls are much thickened owing to the presence of glandular tissue constituting the oviducal gland (*od.g.*).

Traces of the oviducts are often present in the male, particularly near the abdominal openings.

The oviduct in the viviparous forms presents a uterine dilatation and the oviducal gland is much reduced.

In many *Selachii* the nephrostomes of a certain number of the primary kidney tubules persist into the adult as ciliated openings. These are minute in *Scyllium*, but in some forms they attain a considerable size.

The egg is large and heavily yolked. It receives a coat of





are viviparous. The rest are oviparous. In the viviparous forms a thin inconspicuous shell may be formed, but in many there is no shell, and there is a placenta-like interdigitation of folds of the yolk-sac, with corresponding depressions in the uterine walls (*Mustelus*, *Carcharias*).

The mucous membrane of the uterine portion of the oviduct is glandular and in many viviparous forms is raised into villi. In *Pteroplatea micrura*,\* some of these villi are especially long, and dip down into the wide spiracles. Moreover, they possess glands which secrete into the pharynx of the embryo an albuminous fluid, which passes into the intestine and serves as nutriment. In other viviparous forms (e.g. *Myliobatis nieuhofti*, *Trygon*, etc.) the glandular mucosa of the uterus secretes an albuminous fluid, which would appear to enter the alimentary canal of the embryo by the spiracles, and to be absorbed in the intestine. It has been suggested

that the long externally projecting gill-filaments of the embryo, which are highly vascular, may assist in absorbing nutriment from the uterine fluids in the viviparous forms.

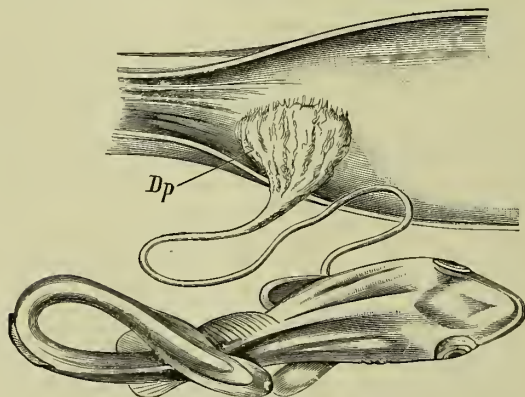


FIG. 82.—Embryo of *Mustelus laevis* connected with the wall of the oviduct by the yolk-sac (from Claus, after J. Müller).

externally (Turner). In other cases sperm is introduced into the female ducts by means of the claspers—though the copulation has rarely been observed. The period of gestation is of considerable length (seven to ten months, or even more), and the young are born or hatched fully developed and of considerable size. The cleavage is partial, closely resembling that of Sauropsida, and there is no larval stage. The development has been largely studied, and throws much light on many morphological problems (e.g. the origin and relations of the excretory organs, of nerves and muscles, cranial segmentation, etc.).

In *Laemargus* the eggs are said to be laid without a shell, and to be fertilised

\* Alcock, *P.R.S.*, 49, 1891, p. 359, and 50, p. 202.

The Elasmobranchii are the most ancient of all known fishes. They make their appearance in the Upper Silurian. They are almost entirely active, carnivorous, predatory fishes and with very few exceptions exclusively marine.

The following is the classification adopted in this work:—

- |       |          |                         |                  |
|-------|----------|-------------------------|------------------|
| Order | 1.       | PLEUROPTERYGII          | (extinct).       |
| „     | 2.       | ACANTHODI               | „                |
| „     | 3.       | ICHTHYOTOMI             | „                |
| „     | 4.       | SELACHII (PLAGIOSTOMI). |                  |
|       | Suborder | 1.                      | Notidani.        |
|       | „        | 2.                      | Squali.          |
|       | „        | 3.                      | Raji (Batoidei). |
| „     | 5.       | HOLOCEPHALI.            |                  |

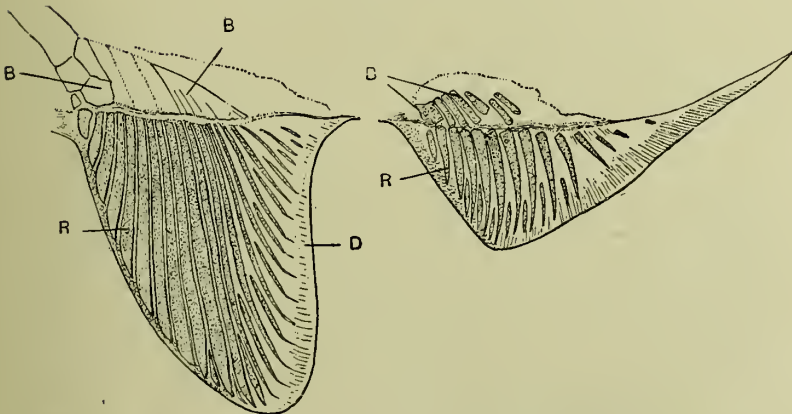


FIG. 83.—*Cladoselache*. A pectoral, B pelvic fins  $\times \frac{1}{4}$ ; B basal somactids within the body-wall, D dermal fin membrane, R peripheral somactids. Left border preaxial (after Dean, from Woodward).

### Order 1. PLEUROPTERYGII.\*

*With unconstricted notochord and heterocercal caudal fin. Paired fins with unsegmented parallel radials, reaching to the edge of the fin. Eyes with a circle of thin dermal plates. Male without claspers on the pelvic fins.*

The skull is unknown, but the jaws are suspended by a slender hyomandibular. The teeth have a principal cusp and several accessory lateral cusps. They resemble teeth which have long been known from the Carboniferous under the generic name *Cladodus*. There were certainly

\* B. Dean, Contributions to the Morphology of *Cladoselache*, *Journ. Morph.*, 9, 1894. Jaekel, Ueber *Cladodus*, *Sitzungsb. d. Gesellsch. naturf. Freunde, Berlin*, 1892. R. Traquair, *Geol. Magazine*, 1888, p. 83.

five gill-arches but there may have been more. Two dorsal fins have been seen (one only shown in Fig. 84), but no anal. The caudal fin is strongly heterocercal; the neural arches are continued to the end of the tail, and carry stout somactids which extend to the edge of the fin. The paired fins are horizontal expansions of the integument. The peripheral somactids are parallel, unsegmented, and extend to the margin; between their distal ends are slender cartilages which are possibly displaced somactid $\delta$ . The basals are also parallel, and are contained

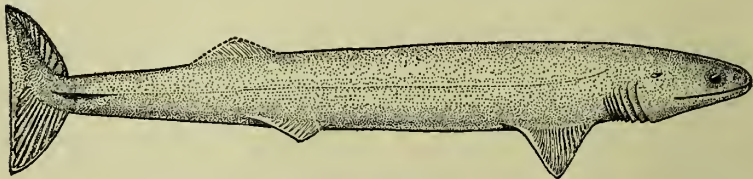


FIG. 84.—Restoration of *Cladoselache newberryi* Dean (from Woodward, after Dean).

in the body wall. The skin is covered by minute denticles, not enamelled. *Cladoselache* Dean, Lower Carboniferous of Ohio; *Cladodus* Ag. for some time known only by teeth; Devonian, Carboniferous, and Permian.

## Order 2. ACANTHODII.\*

With dermal calcareous plates on the skull and pectoral arch, and with a mosaic of quadratic dermal scales on the body. All the fins except the caudal, with a powerful dentine spine on their anterior margin. Without claspers. There are no cranial bones, nor membrane bones connecting the pectoral arch with the cranium.

This group, which was formerly placed with the Ganoids, is now placed with the Elasmobranchs. The endoskeleton contains granular calcifications, and the dermal plates placed on the head, body and pectoral girdle



FIG. 85.—*Acanthodes Wardi*  $\times \frac{1}{4}$  (after Woodward). The orbit is made too small and the gill-frills are hypothetical.

seem to have consisted of vaso-dentine or of structureless lamellae without bone-cells. The most marked characteristic of the group is the large

\* Huxley, *Geological Survey of the United Kingdom*, 10, 1861. Fritsch, *Fauna der Gaskohle in Böhmen*, 2, 1889. Reis, *Zur Kenntniss des Skelets der Acanthodinen*, *Geognost. Jahreshefte*, München, 1890, 1894. Traquair, *Geol. Mag.*, 1888, p. 511; 1889, p. 17.

spines on the front of the fins. These appear to have consisted of dentine, and are doubtless comparable to the spines found in similar positions in the fins of Elasmobranchs. It is probable that a number of isolated spines which have received special generic names (*Onchus*, *Byssacanthus*, *Homacanthus*, etc.) may have belonged to fishes of this group, and that a number of quadratic scales, *e.g.* *Thelolepis*, *Coelolepis*, etc., from the Upper Silurian, were part of the dermal armature of similar fishes. Pectoral and pelvic fins are always found.

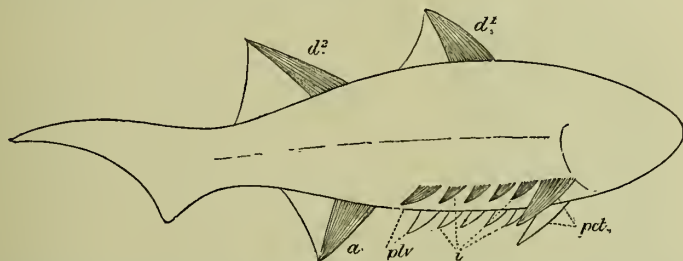


FIG. 86.—*Climatius scutiger*, outline of fish with spines shaded. The pectoral fins spines *pc* are the two large spines next the head; then follows a double row of smaller spines *i*, the last of which are the pelvic fin-spines *plv*. The large fin with spine *a* between the paired spines and the caudal fin is the anal; *d*<sup>1</sup>, *d*<sup>2</sup> dorsal fins.

The eye is surrounded by dermal plates; the notochord must have been persistent; the supports of the fins are not preserved; the tail is heterocercal and the caudal fin without any trace of upper lobe. Comparatively small fishes. *Acanthodes* Ag. (Fig. 85), Lower Devonian to Lower Permian; *Diplacanthus* Ag., and *Climatius* Ag., Upper Silurian and Lower Devonian, without teeth, with four or five pairs of spines between the pectoral and pelvic fins (Fig. 86). Most of the sub-order do not show teeth, but there is a powerful dental armature in *Ischnacanthus*.

### Order 3. ICHTHYOTOMI.\*

*The cartilaginous endoskeleton is permeated by granular calcifications; notochord uncontracted, with slight calcifications in its sheath; neural and haemal arches calcified, with long spinous processes; tail diphycercal; pectoral and pelvic fins with long segmented axis and biserial radii; pelvic fins with claspers in the male. The teeth have two large lateral cusps, with one small median cusp. Lower Carboniferous to Lower Permian.*

*Pleuracanthus* Ag. (*Xenacanthus* Beyr.) (Fig. 87). Body elongated, to half a metre; skin probably naked, with a long spine attached to the occipital region of the cranium; five, possibly seven, branchial arches; all the fins with dermatotrichia; pectoral girdle arch-like, united with its fellow, composed of two pieces; pectoral fin (Fig. 76) with segmented axis; rachistichous and pleurorachic, or nearly so (p. 57); pelvic fin similar, but with no postaxial somactids, with claspers; pelvic girdle of two separate arches. The somactids of the long dorsal fin are segmented

\* Fritsch, *loc. cit.* Davis, On the Fossil Fish Remains of the Coal Measures in the Brit. Islands, I. *Pleuracanthidae*, *Trans. Roy. Dublin Soc.*, 4, 1892.



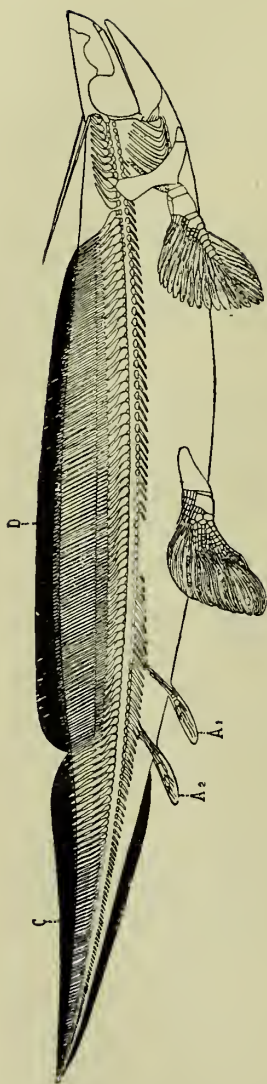


FIG. 87.—*Pleuracanthus decheni*, restored by A. Fritsch,  $\times \frac{1}{2}$ ; Lower Permian, Bohemia (from Woodward).  $A^1$ ,  $A^2$  anal fins;  $C$  dorsal part of caudal fin;  $D$  dorsal fin. The specimen from which this figure was taken has been crushed in such a way that the paired fins appear to have their postaxial sides turned forward.

into three pieces, and are twice as numerous as the neural arches, those of the dorsal part of the caudal fin are similar, but equal in number to the neural arches; the anal fin is double, and its supports are partly fused, and branch peripherally. *Didymodus* Cope, Permian of Texas, skull shows symmetrical fissuring, to which the name of the sub-order is due.

#### Order 4. SELACHII (PLAGIOSTOMI),

*Elasmobranchii* with characters of the soft parts as defined for the subclass, with hyostylic skull (except Notidanidae) and heterocercal tail. The notochordal sheath is always segmented, though sometimes imperfectly; the pectoral fins with three basal cartilages, and the pelvic fins of the male with claspers.

The mouth is placed on the under surface of the head, except in *Chlamydoselachus* in which it is sub-terminal, and *Rhinodon* and *Rhina* in which it is terminal. The skin has detached placoid scales only. The body is either fusiform or flattened dorsoventrally, and there is usually a spiracle, but the pseudobranch is absent in the *Scymnidae*, *Lamnidae*, *Myliobatis*, *Trygon*, etc. In *Carcharias* and *Zygaena*, in which the spiracles are absent, a pseudobranch is present buried in the flesh or placed on the front wall of a recess of the mouth. They are almost all marine, but a few ascend American and Asiatic rivers, and a few are confined to freshwater (some *Trygons*, two species of *Carcharias*). They have existed since Palaeozoic times



## Sub-order 1.

**NOTIDANI.**

With six or seven branchial apertures and a small spiracle with one dorsal fin without spine. Vertebral column imperfectly segmented. Caudal fin without a pit at its root; without labial fold and nictitating membrane.

Fam. 1. **Chlamydoselachidae**.  
Body eel-like; mouth anterior; nasal opening divided and on side of head; lateral line as an open groove on the body, but closed (with openings left) on the head; with six gill openings and six branchial arches; opercular fold (first gill-cover) free across the isthmus; the

palatoquadrate is not articulated with the post-orbital process of the skull and there is a large hyomandibular; notochord unconstricted posteriorly; teeth similar in both jaws, each with three slender, curved cusps separated by a pair of rudimentary denticles on a broad base; viviparous. *Chlamydoselachus* Garman, from the deep sea, 5-6 feet. Japanese seas, Atlantic and Arctic.

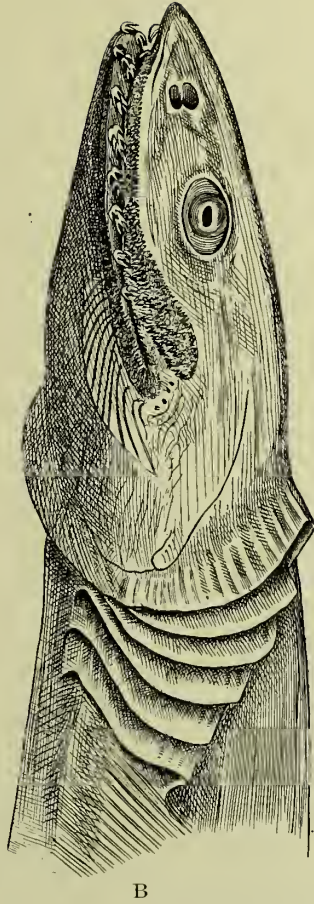


FIG. 88.—A. *Chlamydoselachus anguineus* Garman; B. side view of the head of the same (after Garman).

\* Garman, *Bull. Mus. Zool. Harvard College*, 12, 1885.

Fam. 2. **Notidanidae**. Mouth sub-inferior; nostrils on lower side, nearer snout than mouth; dentition unequal in the two jaws; in the upper jaw one or two pairs of awl-shaped teeth, the next six teeth broader and each provided with several cusps, one of which is the strongest; lower jaw with six large, comb-like teeth on each side, beside the smaller posterior teeth; viviparous; sometimes reach a large size. The palatoquadrate articulates with the postorbital process of the skull and the hyomandibular is comparatively slender; each segment of the vertebral column of the middle part of the trunk region carries two neural arches and corresponds to two pairs of spinal nerves (p. 126); the pseudobranch is very large and has several well-developed laminae. Temperate and warm seas. *Hexanchus* Raf., with six pairs gill-apertures; vertebrae without calcification; *H. griseus* Gmelin, 8-26 feet, Mediterranean, W. coast Scotland; *Heptanchus* Raf., with seven pairs gill-apertures, vertebrae asterospondylous.

### Sub-order 2. **SQUALI**.

Vertebral column well segmented, vertebrae amphicoelous with a double cone of calcified cartilage, outside which and springing from it there may be radiating calcareous lamellae (asterospondylous) or additional concentric calcified rings (cyclospondylous); with two dorsal fins, and with or without anal fins. With five gill apertures laterally placed, spiracle present or absent, never large. The palatoquadrate is not articulated directly to the skull except in *Cestraciontidae*.

This sub-order includes the great body of living sharks, and has existed since the Silurian period. Some of the living genera have existed since early times; e.g. *Cestracion*, Upper Jurassic; *Scyllium*, and *Scapanorhynchus* (*Mitsukurina*) Cretaceous; *Pristiurus*, Upper Jurassic. Most of them are active predatory creatures, and some attain a considerable size. The largest are however harmless creatures, which like the whalebone whales exist on small marine organisms which are detained on their prolonged gill-rakers (*Selache*, *Rhinodon*).

Fam. 3. **Cestraciontidae**. Bull-head sharks; asterospondylous; the palatoquadrate articulates by an extensive surface with the preorbital region of the skull; two dorsal fins with spines, the first dorsal opposite the space between pectorals and pelvis, the second in advance of the anal; upper lip divided into seven lobes, the lower with fold; spiracle small, below posterior part of eye; without nictitating membrane; dentition similar in both jaws, viz. small obtuse teeth in front, pointed and provided in young individuals with three to five cusps; lateral teeth large, pad-like, twice as long as broad; Pacific and East Indian Archipelago; size small; oviparous, egg-case spirally twisted. *Cestracion* Cuv. (*Heterodontus* Blainv.), *C. phillipi* Blainv., Port-Jackson shark.

Extinct genera are *Orodus* Ag., *Campodus* de Kon., *Sphenacanthus* Ag., Carboniferous Limestone; *Hybodus* Ag., Trias to Cretaceous; *Palaeospinax* Eg., Lias; *Acrodus* Ag., Trias to Cretaceous, etc.

Fam. 4. **Scylliidae.** Dog-fishes; asterospondylous, dorsal fins without spine; first dorsal above or behind the pelvic; an anal fin; no membrana nictitans; spiracle distinct; mouth inferior; teeth small; nostrils near the mouth, sometimes confluent with it, sometimes with cirri. *Scyllium* Cuv. (*Scylliorhinus* Blainv.), upper edge of caudal fin smooth; *Sc. canicula* Cuv., small-spotted dog, single nasal flap, pelvic fins separated; eggs laid in April, hatched in December; *Sc. catulus* Cuv., large-spotted dog, nurse hound, nasal flap divided, pelvic fins almost conjoined; *Pristiurus* Bon., snout much produced, small flat spines along upper edge of caudal fin, *P. melanostomus* Bon.; *Ginglymostoma* M. and H., large sharks of the warm seas, nostrils confluent with mouth; *Stegostoma* M. and H., tiger-shark to 15 feet, India; *Parascyllium* Gill, Tasmania, 2½ feet; *Chiloscyllium* M. and H., nasal and buccal cavities confluent, Indian and Australian, 2½ feet; *Crossorhinus* M. and H., Australia and Japan to 10 feet, mouth nearly anterior, nasal and buccal cavities confluent, Extinct genera: *Palaeoscyllium* Wagn., Upper Jurassic; *Mesiteia* Kramb., Cretaceous.

Fam. 5. **Carchariidae.** Asterospondylous; first dorsal opposite space between pectoral and pelvic, without spine; an anal; with nictitating membrane; mouth crescentic, inferior; spiracles present or absent. *Carcharias* M. and H. (sub-genera, *Scoliodon* M. and H., *Physodon* M. and H., *Aprionodon* Gill, *Hypoprion* M. and H., *Prionodon* M. and H.) comprises the true sharks; no spiracle; teeth with a single cusp, snout produced, pit at root of tail; temperate and tropical; *C. glaucus* Cuv., blue-shark, 25 ft.; *C. gangeticus* of the Ganges and inland lakes of the Fiji Islands, and *C. nicaraguensis* G. and B., Lake Nicaragua, only freshwater sharks known, 7 ft.; *Hemigaleus* Bleek, East-Ind. Archipelago; *Loxodon* M. and H., Ind. Ocean; *Galeocерdo* M. and H., arctic, temp. and trop. seas; *Thalassorhinus* M. and H., Med. and Atl.; *Galeus* Cuv., small spiracle, teeth with single cusp, snout elongated, no pit at root of tail, temp. and trop., viviparous; *G. canis* Rond., tope, whitohound, penny dog, miller's dog, 7 ft.; *Zygaena* Cuv. (*Sphyrna* Raf.), temp. and trop., no spiracles, hammer-headed sharks, eyes at extremity of head lobes; *Z. malleus* Shaw, hammer-shaped head, viviparous, balance fish; *Triaenodon* M. and H., no spiracles, Red Sea, Ind. Ocean; *Leptocarcharias* Smith, no spiracles, S. Africa; *Triacis* M. and H., Ind. and Pac. Oceans; *Mustelus* Cuv., viviparous, teeth flat and paved, temp. and trop. seas, spiracles small, no pit at root of tail, bottom-fish; *M. laevis* Risso, embryo attached to uterus by placenta; *M. vulgaris* M. and H., no placenta, 6 ft., smooth hound, skate-toothed dog. *Scylliogaleus* Blgr., Natal.

Fam. 6. **Lamnidae.** Mackerel sharks. Large sharks with large teeth; first dorsal opposite space between pectoral and pelvic, without spine; asterospondylous; an anal fin; no nictitating membrane; mouth crescentic, inferior; spiracles absent or minute, varying even in the same species; pelagic, attain large size. *Lamna* Cuvier, Porbeagles, teeth lanceolate, large, with smooth edges, keel at side of tail, temperate and tropical seas; *L. cornubica* Gmelin, Porbeagle (porpoise and beagle) or Beaumaris shark, viviparous, 10 ft.; *Carcharodon* M. and H., *C. rondeletii* M. and H., great blue-shark, man-eater, spiracle minute or absent, Med. to

Australia, 36 ft.; *Odontaspis* L. Ag., temp. and trop. seas; *Alopecias* (*Alopias*) M. and H., teeth triangular, flat, smooth edges, caudal fin long, no keel at side of tail, temp. and trop. seas; *A. vulpes* Gmelin, thrasher-shark, fox; *Selache* Cuv. (*Cetorhinus* Blainv.), teeth small, numerous, conical and smooth, keel at side of tail, whalebone-like gill-rakers consisting of dentine on the gill-arches, Arctic to Med.; *S. maximus* Gunner, basking-shark, sun-fish, one of the largest of living fishes, to 40 ft., large gill apertures, vertebrae appear to be tectospondylous, owing to presence of a number of concentric lamellae in the adult; inoffensive, of great strength, has been known to tow a 70-ton boat against a fresh gale; a large fish yields  $1\frac{1}{2}$  tons of oil; *Pseudotriacis* Capello. *Mitsukurina* Jordan (*Scapanorhynchus* S. Wood), Japan. Extinct genera: *Orthacodus* S. Wood, Jurassic and Cretaceous; [*Odontaspis* Ag., Upper Cretaceous.] (*line 1*),

Fam. 7. **Rhinodontidae.** Whale-sharks; asterospondylous; origin of first dorsal fin in front of pelvic; the second small, opposite the anal, both without spines; a pit at root of caudal; side of tail with keel; spiracle small; membrana nictitans absent; mouth and nostril near the front of snout; teeth small; gill openings wide, with gill-rakers, Cape of Good Hope, Seychelles, Japan. *Rhinodon* Smith; a gigantic shark known to exceed 50 ft., said to attain 70 ft.

Fam. 8. **Spinacidae.** Cyclospondylous; spiracles present; gill openings narrow; without nictitating membrane; a deep groove along either side of the mouth; a spine on front side of each dorsal fin; without anal fin. *Centrina* Cuv. (*Oxynotus* Raf.), body somewhat three-sided with a fold of skin at each angle, teeth in lower jaw triangular, erect and with finely serrated edges, no membrana nict., Med. and adjacent Atlantic; *C. Salviani* Risso, attains to 4-5 ft.; *Acanthias* Risso (*Squalus*), teeth rather small, their points placed so obliquely that their inner margin which is smooth forms the cutting edge, no membrana nict., temp. seas of both hemispheres; *A. vulgaris* Risso, picked dog-fish, spur-, spear-, or bone-dog, hoe, skittle-dog; viviparous; *Centrophorus* M. and H., Eur. seas, Moluccas; some species live at a great depth (400-500 fathoms); *Scymnodon* Boc and Cap.; *Spinax* Cuv. (*Etmopterus* Raf.), Eur. Seas, W. Indies; *Centroscyllium* M. and H., Greenland, has been taken 300-400 fathoms.

Fam. 9. **Scymnidae.** Like Spinacidae, but no spines on dorsal fins; *Scymnus* Cuv., Med. and Atlantic; *Laemargus* M. and H. (*Somniosus* Le Sueur), teeth in upper jaw small and conical, those in lower jaw in several rows, their points placed so obliquely that their inner margin, which is smooth, forms the cutting edge; *L. microcephalus* Kröyer (*borealis* M. and H.), Greenland shark; notochordal sheath imperfectly segmented, uncalcified (calcified and segmented in *L. rostratus*); attains 25 ft., bites pieces out of whales; with two pyloric caeca; eggs large, soft, globular, without shell, dropped in the ooze on the sea bottom, said to be fertilised externally; they breed at considerable depths (100 fathoms); *Euprotomicros* Gill, Ind. Ocean; *Echinorhinus* Blainv., skin with irregularly placed round osseous tubercles, teeth large, oblique, with several small cusps on each side of the main one, Med. and Atl., *E. spinosus* Blainv., to 8 ft.; *Isistius* Gill.

Fam. 10. **Rhinidae.** Ray-like sharks. Tectospondylous; spiracles large, gill openings wide, lateral, and partly concealed from above by pectoral fins; body flat; mouth anterior; nostrils at front end of snout



with skinny valvular coverings ; pectoral fins large, laterally expanded, but not attached to head ; dorsal fins spineless, in caudal region, no anal ; males with claspers ; temperate and tropical seas ; intermediate between the sharks and rays. *Rhina* Klein (*Squatina* Dum.), angel-fish, monk-fish, viviparous, to 8 ft.

Fam. 11. **Pristiophoridae** probably here. Shark saw-fish. Rostral cartilage produced into long flat lamina, armed along each edge with teeth ; *Pristiophorus* M. and H., Japan, Australia.

### Sub-order 3. **RAJI (BATOIDEI).**

Gill openings ventral, five in number ; spiracle always present, without anal fin ; dorsal fins, if present, on the tail ; vertebrae tectospondylous. Skates and Rays.

The body is much flattened dorso-ventrally and the pectoral fins are enormously expanded in an antero-posterior direction. The five branchial apertures are entirely on the ventral surface of the body. The spiracles are dorsally placed behind the eyes ; they are wide and can sometimes be closed by a valve. It is probable that they are used for the intake of the respiratory water when the fish is lying on the ground. The caudal region is usually slender, and in some forms very much so. There is no anal fin, and the dorsal fins when present are placed on the tail.

The *Pristidae* and *Rhinobatidae*, which have a well-developed caudal region and are intermediate in the form of their body between the sharks and rays, are powerful swimmers, but most of the Raji lead a more sedentary life on the bottom, rarely coming to the surface. They feed chiefly on *Mollusca* and *Crustacea*. A few deep-water forms are known, but they are rarely taken below 100 fathoms. Most are shore-forms. The *Myliobatidae*, which include the largest forms in the sub-order, are however met with in the open sea. Some species are confined to fresh water. They are for the most part oviparous. The flesh of many of the species is eaten. Some of the living families have existed since the Jurassic.

Fam. 1. **Pristidae**. Saw-fishes. Snout much produced (rostral process of cranium) with lateral saw-like teeth ; body somewhat shark-like, the disc-like body gradually passing into the tail, which is comparatively thick, with two dorsal fins and a caudal fin, without serrated caudal spine. *Pristis* Latham, tropical and sub-tropical, attain a considerable size, with a saw 6 ft. long and 1 ft. broad at base.

Fam. 2. **Rhinobatidae**. Tail long and strong with two dorsal fins, a caudal and a longitudinal fold on each side, without serrated caudal spine ; rayed portion of pectoral fins not continued to snout ; no electric



organ ; viviparous. *Rhinobatus* Bl. and Schn., guitar-fishes, tropical and sub-tropical, and fossil from the upper Jurassic ; *Rhynchobatus* M. and H., Ind. Ocean to China ; *Trygonorhina* M. and H., Australia ; *Zapteryx* Jor. and Gilb., Peru ; *Platyrhinoidis* Gar., California. Extinct genera : *Asterodermus* Ag., *Belemnobatis* Thiol., Upper Jurassic.

Fam. 3. **Torpedinidae.** Trunk a broad, smooth disc ; tail with rayed dorsal (absent in *Temera*) and caudal fins and a longitudinal fold on each side, without serrated dorsal spine ; anterior nasal valves confluent into a quadrangular lobe. An electric organ between the pectoral fins and the head. Eocene to the present time. *Torpedo* Dum. (*Narcobatis* Blainv.), large specimens (width from 2 to 3 ft.), can disable a man. Med., Atl., Ind. Oceans ; *T. nobiliana* Bon., spiracles not fringed at their margins ; on flat sands or mud, 40-50 fathoms ; *T. marmorata* Risso, spiracles fringed ; *Narcine* Henle, trop. and sub-trop. ; *Hypnos* Dum., Australian ; *Discopyge* Tschudi, Peru ; *Astrape* M. and H., Ind., S. Afr. ; *Temera* Gray, E. Ind.

Fam. 4. **Rajidae.** Skates. Disc broad, rhombic, generally with asperities or spines ; tail with longitudinal fold on each side ; pectorals extend to snout ; no electric organ or serrated caudal spine ; oviparous ; sexual differences are frequently observable, in colour, form of teeth and arrangement of spines. Cretaceous to the present time. *Raja* Art., tail distinct from disc, pectoral fins not extended to front end of snout, caudal fin rudimentary ; may attain width of 6-7 ft. ; in some species the teeth of the male are sharper than in the female, and in all species the males are armed with patches of claw-like retractile spines on the upper side of the pectoral fin ; seas of both hemispheres ; *R. batis* L., skate, oviposition from May to September, to 6-7 ft. ; *R. macrorhynchus* Raf., flapper skate ; *R. alba* Lacép., white skate, to 8 ft. ; *R. oxyrhynchus* L., long-nosed skate ; *R. fullonica* L., Fuller's ray, shagreen skate ; *R. clavata* L., thornback ; *R. maculata* Montagu, homelyn ray, spotted ray ; *R. microcellata* Montagu ; *R. radiata*, starry ray ; *R. circularis* Couch, sandy ray. *Psammobatis* Günth., South America ; *Sympterygia* M. and H. ; *Platyrrhina* M. and H. Extinct genus : *Cyclobatis* Eg., Cretaceous.

Fam. 5. **Trygonidae.** Sting-Rays. Pectorals continued to and confluent at end of snout ; tail long and slender, without lateral folds ; vertical fins none or imperfect, often replaced by strong serrated spine. Tertiaries to present time. *Urogymnus* M. and H., Ind. Oc. ; *Ellipsurus* Schomburgk ; *Trygon* Adanson (*Dasyatis* Raf.), tail with long serrated spine, temp. and trop. ; *T. pastinaca*, sting ray, sandy ground near land, caudal spine causes severe wounds ; *Taeniura* M. and H., Indian seas, fresh-waters of trop. America ; *Urolophus* M. and H., Australian and Caribbean seas ; *Pteroplatea* M. and H., temp. and trop. seas.

Fam. 6. **Myliobatidae.** Eagle-rays. Disc broad with large pectoral fins which are not present at the sides of the head, but reappear as at the extremity of the snout as a pair of detached fins ; teeth hexagonal, flat, tessellated ; tail long, thin, whip-like ; viviparous. *Myliobatis* Cuv., snout with a soft prolongation with fin rays ; temp. and trop. seas ; *M. aquila* L., mill-skate, whip-ray, eagle-ray ; *Aetobatis* M. and H., tropical seas ; *Rhinoptera* Kuhl, trop. and sub-trop. seas ; *Dicerobatis* Blainv. (*Aodon* Lac.) (*Cephaloptera* Dum.), head with a forward-pointing horn-like projection on either side ; attain great size ; temp. and trop. seas ; *D. giornae*. *Ceratoptera* M. and H. (*Manta* Bancroft),

temp. and trop. seas, attain great size, 20 ft. wide. Last two genera often called sea-devils. Extinct genera: *Ptychodus* Ag., Cretaceous; *Promyliobatis* Jaekel, Eocene.

The following extinct Palaeozoic families are placed here:—

COCHLIODONTIDAE, with several genera, from the Carboniferous Limestone; PSAMMODONTIDAE, from the Carboniferous Limestone; and PETALODONTIDAE, also from the Carboniferous.

### Order 5—HOLOCEPHALI.\*

*Without spiracle, with four clefts covered by an opercular fold which contains a cartilaginous plate. The skull is autostylic, and the notochordal sheath is unsegmented. There are two dorsal fins and an anal.*

The *Holocephali* differ from the *Plagiostomi* in the fact that there are only four gill clefts (though there are five branchial

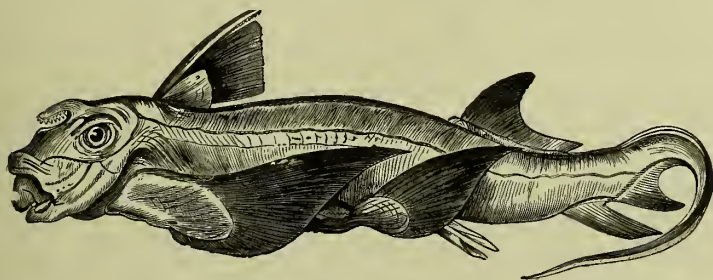


FIG. 89.—*Chimaera monstrosa* (Règne Animal).

arches). Moreover the gill apertures are covered by an opercular fold, and the palatoquadrate bar is continuous with the skull in its whole extent. They have a cartilaginous skeleton and claspers on the pelvic fins of the male.

The mouth is small, ventral, and bounded by lip-like folds supported by labial cartilages. The nostrils are confluent with the mouth. The urogenital part of the cloaca is separate from the rectum and opens behind the anus. The anterior dorsal fin has a strong spine, on its front border, which is attached to the fused neural spines of the anterior vertebrae. The tail is heterocercal and prolonged in *Chimaera* into a long filament. There

\* G. Good and T. H. Bean, *Oceanic Ichthyology, Memoirs of the Museum of Comp. Anat. Harvard College*, 22, 1896. A. A. W. Hubrecht, *Kennis des Kopfskelet d. Holocephalen, Nederland Arch. Zool.*, 3, 1877. S. Garman, *The Chimeroids, Bull. Mus. Harvard Coll.*, 43, 1904.

is on each side in the male a peculiar structure consisting of a plate carrying teeth and sunk in a pit just in front of the pelvic fin.

The head of the male is provided with an erectile hook-like process projecting forwards over a groove and armed on its lower surface with small spines. The skin is usually naked except in the young, in which small placoid spines are found principally in a double row on the back. The lateral line may be an open groove (*Chimaera*) or a closed canal (*Callorhynchus*). In *Chimaera* the lips of the groove are approximated on the head (Fig. 42), but remain apart at intervals giving the appearance of openings. Ampullary canals are present as in Plagiostomes. The eyes are without lids.

The notochordal sheath is thick, cartilaginous and unsegmented. It contains in *Chimaera* numerous calcified rings (four or five to each segment). The arch tissue is segmented, except in the front and in the whip-like tail, and does not meet round the notochord sheath, except again at the front end and in the tail. The neural arches consist of two pairs of pieces and a dorsal piece for each pair of spinal nerves. The neural spine of the anterior fused arch tissue is large and carries the anterior dorsal fin, the basals of which are fused into one piece.

The skull is autostylic (p. 63), has rostral continuations and is without the prefrontal fontanelle. It has a well marked membranous interorbital septum, which is placed dorsal to the brain. It articulates with the vertebral column by two condyles. The auditory capsule is incomplete internally so that the space for the membranous labyrinth is open to the cranial cavity. There are three pairs of labial cartilages and the hyoid arch which carries branchial rays is attached by ligament to the skull. There are five branchial arches. The hyoid arch carries a demibranch (uniserial), the first three branchials each have a holobranch (biserial), and the fourth branchial carries a demibranch. There is no gill-cleft between the fourth and fifth branchial arches. The gill filaments are attached as in Plagiostomes and do not project.

The paired fins and their girdles are formed on the Plagiostome type, except that the two halves of the pelvic girdle are united only by ligament.

The teeth are large and few in number consisting of strong

plates with cutting edges. There are two pairs in the upper and one pair in the lower jaw. The intestine has a spiral valve and the anus is in front of the urogenital aperture. There is a conus arteriosus with three rows of valves.

The brain is characterised by the great length of the thalamencephalon, and the cerebrum is very small. The olfactory peduncles are long and there is an optic chiasma. The pineal body is as in Plagiostomes, and there is an extracranial part of the pituitary body lodged in a pit on the base of the skull. The cranial nerves\* are arranged in the usual manner; the roots of the fifth and seventh are more distinct than in most fishes.

There is a pericardio-peritoneal canal.

The urogenital organs appear to be similar to those of Plagiostomes. In the female the shell gland is large. In the male there is a large vesicula seminalis, and the müllerian ducts are complete tubes opening at each end.

They are oviparous and have large eggs. The eggshell is covered with hair-like processes, and may attain a great size. They are probably laid in deep water, where the young are for the most part found.

They have existed since the Jurassic period.

In many points of structure these animals depart from other Elasmobranchs, and they have by some authorities been removed from that group and raised to the rank of a sub-class with affinities to the Dipnoi by the characters of their skull and teeth. There is much to be said for this view, for they present affinities to more than one piscine sub-class: to Elasmobranchs by their placoid scales, cartilaginous skeleton, absence of membrane bones, their gill-laminae, the open otocyst, the ampullary canals, the form of the brain, the structure of the urinogenital organs, their fin skeleton and claspers, and by their large eggs and development: to the Ganoids by the separation between the urinogenital sinus, and the alimentary canal, and by the incomplete internal wall of the auditory capsule: and to the *Dipnoi* by the last-named feature, by their autostylic skull, their peculiar teeth, and their vertebral column. They differ from Elasmobranchs and resemble Ganoids and Dipnoi in having an operculum, but they stand by themselves in having only four branchial clefts and a

\* F. J. Cole, Cranial Nerves of *Chimaera*. *Trans. Roy. Soc. Edinburgh*, 38, 1896, p. 631.

demibranch on the fourth branchial arch. It is clear from this that the Elasmobranch characters strongly predominate, and in our opinion they may fairly be retained as an order of that subclass.

*Chimaera* L., snout soft, prominent, without appendage; tail produced into a fine filament; deep water (200 to 1,200 fathoms) of coasts of Europe, N. Pacific, Cape; *C. monstrosa* L., King of the Herrings; attains 3 or 4 ft.

*Hydrolagus* Gill, like *Chimaera*, but three dorsals and caudal, and tail without filament; surface waters, N. Pacific.

*Callorhynchus* Gronov. Snout with a cartilaginous prominence ending in a cutaneous flap; S. Pacific, Cape; egg-case 9 or 10 in.  $\times$  3 in.

*Hariotta* Goode and Bean. Snout elongated, no frontal clasper, anal fin as cutaneous fold, deep water 700 to 1,200 fathoms.

Extinct genera\*: *Ischyodus* Eg., Upper Jurassic and Lower Cretaceous; *Ganodus* Ag.; *Edaphodon* Buckl., Cretaceous, Eocene, Oligocene; *Pachymylus* Smith, Upper Jurassic, etc.

The extinct families PRYCTODONTIDAE, known by teeth from the Devonian; SQUALORAJIDAE, known by its skeleton, from the Lias; MYRIACANTHIDAE, also known by skeletons from the Lias and Upper Jurassic, are placed here.

\* E. T. Newton, Chimaeroid Fishes of the British Cretaceous Rocks, *Mem. Geol. Soc. U. Kingdom*, 1878.



## CHAPTER VII.

### SUB-CLASS GANOIDEI. \*

*Fishes with a conus arteriosus, optic chiasma, free pectinate gills and an operculum, abdominal pelvic fins, a spiral valve in the intestine, an air-bladder, and without a processus falciformis and choroid gland. The oviducts and urinary ducts unite and open by a common urogenital aperture behind the anus. The skull is hyostylic and is without a supraoccipital bone. The segmentation of the ovum is complete, a pronephros is present in the larva and abdominal pores are always found.*

Very few of the characters mentioned in the definition are peculiar to Ganoids: they are almost all found in *Teleostei* or *Elasmobranchii*. This fact coupled with the great variations of structure found in the group points to the conclusion that the sub-classes, *Elasmobranchii*, *Teleostei*, *Ganoidei* and *Dipnoi* are the survival of a once great and continuous group of animals, a large number of which have become extinct, leaving three groups, *Elasmobranchii*, *Teleostei* and *Dipnoi*, each fairly compact and showing but little variety of organization, and one, the *Ganoidei*, loose and heterogeneous with large gaps between the individual members. Although it may fairly be held that by such forms as *Lepidosteus* and *Amia* the Ganoids more nearly approach the *Teleostei* than the *Chondrostei* do the *Elasmobranchii*; we cannot

\* J. Müller, Ueb. d. Bau u. d. Grenzen der Ganoiden, *Abh. d. Berlin Akad. d. Wiss.* 1844; id. Myxinoiden, *op. cit.* J. Hyrtl, Ueb. den Harnwerkzeuge bei den Ganoiden, *Wien Denkschriften*, 8, 1855. Lütken, Ueb. d. Begrenzung und Eintheilung d. Ganoiden, *Palaeontographica*, 22, 1872. Huxley, 'The systematic arrangement of the fishes of the Devonian Epoch,' *Mem. Geolog. Survey*. London, 10, 1861; and 12, 1866. Traquair, *Ganoid fishes of the British Carboniferous Formations*, *Palaeontogr. Soc.* 1877. V. Wijhe, Visceral Skel. u. Nerven des Kopfes der Ganoiden u. *Ceratodus*, *Nied. Arch. Zool.*, 5, 1882, p. 207. Zittel, *Grundzüge d. Palaeontologie*, Leipzig, 1895 (English Translation, Macmillan, 1902). Smith-Woodward, *Outlines of Vert. Palaeontology*, Cambridge, 1898.

agree with those zoologists who wish to unite the Ganoids and Teleosteans into a single group, distinct from other piscine orders. In this opinion we are in company with two of the greatest anatomists of the last century, J. Müller and F. M. Balfour. The latter has expressed his view in words, with which we are in entire agreement and which we quote here, because they appear to express in the most judicial form the state of the question. He says, "We do not recommend such an arrangement (union of the Ganoids and Teleosteans) which in view of the great preponderance of the *Teleostei* amongst living fishes would be highly inconvenient, but the step from *Amia* to the *Teleostei* is certainly not so great as that from the *Chondrostei* to *Amia*, and is undoubtedly less than that from the *Selachii* to the *Holocephali*."

The scales present some variation in arrangement and structure. In the living *Chondrostei* they may be almost absent on the body as in *Polyodon*, or arranged in rows as in *Acipenser*; not, however, forming a continuous cuirass except in the caudal region. They frequently carry bony spines, which are without any enamel cap. In some extinct *Chondrostei* they form a continuous cuirass, and have often the rhombic form typical of the order. In *Crossopterygii* they form a continuous armour and are either rhombic or cycloid; in the living forms it can be shown that they are coated externally by ganoin and that in some cases they carry spines which consist of cones of dentine capped with enamel. In *Lepidosteii* there is also a continuous armour of rhombic or cycloid scales, and in the living *Lepidosteus* it has been shown that these scales are coated with ganoin (*γavos* sheen) and may, especially in the young state, carry one or a number of small spines having exactly the structure of the spine of a placoid scale.

In *Amia* the scales, which form a complete armour, are Teleostean in character and consist of bony plates without ganoin. Moreover it has been shown from a study of living forms that the scales save for the toothlike projections which occur in *Polypterus* and *Lepidosteus* are purely mesodermal products, and that the ganoin which was formerly thought to be enamel is really of the nature of vitrodentin and is formed by the scleroblasts\* of the dermis.

\* Scleroblasts are cells which secrete a hard skeletal substance.

Although the scales are dermal structures, they are said to be frequently exposed on the surface in the adult. This, if true, must be due to the fact that the overlying epidermis and dermis have been rubbed off. This may frequently happen in the handling of animals during their preservation.

**Vertebral column.** In the *Chondrostei* the notochord is persistent and its sheath is stout but unsegmented and unossified. The neural and haemal arches on the other hand are segmented; they are attached to the sheath but do not extend round it. In other living Ganoids (for the vertebral column of extinct genera the reader is referred to the special accounts), vertebral bodies are formed by the extension of the arch tissue round the sheath, its chondrification, segmentation and ossification. In *Polypterus* and *Amia* the vertebral bodies are amphicoelous as in Teleosteans; in *Lepidosteus* they are concave behind and convex in front (opistho-coelous).

In some extinct Ganoids (Fig. 90A) bony plates are found, corresponding to each arch, on the ventral side of the notochord. They are called

**hypocentra**, and carry the haemal arches. A corresponding plate, which may be composed of two pieces, is found on the dorsal side, and called **pleurocentrum**. Such incipient vertebrae are called *half-vertebrae*. They may, each of them, extend completely round the notochord (Fig. 90B), as in the tail of the living *Amia*, in which case one of them only carries the neural and haemal arches. *Ring-vertebra* is the term used when the pleurocentrum and hypocentrum are joined to form a ring round the notochord, as in the amphicoelous vertebrae of *Polypterus*, *Teleostei*, etc., in which the bony ring has thickened so as to constrict the notochord in the middle of each vertebra. In *Lepidosteus* the arches are continuous with the bony centrum. In all other Ganoids with bony centra the arches are separated from the centra by persistent cartilage.

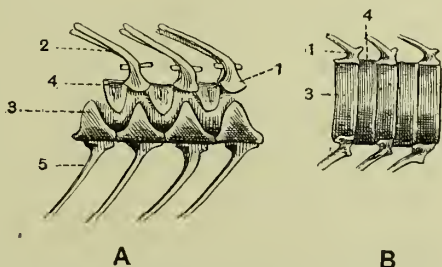


FIG. 90.—A. Vertebra of *Caturus furcatus*. B. Caudal vertebrae of *Eurycormus speciosus* (after Zittel). 1 neural arch; 2 the bifurcated neural spine; 3 hypocentrum; 4 pleurocentrum; 5 rib.

The caudal fin is diphyccercal in *Polypterus*. In other living genera it is heterocercal. In *Amia* it is *hemiheterocercal* (externally homocercal, internally heterocercal), and the dorsal lobe of the caudal fin is reduced to the covering of fulcrum.

The structure of the skull is very varied, but the cartilaginous cranium always contains cartilage bones and is invested by membrane bones. The dorsal membrane bones are dermal structures and are frequently in the adult exposed on the surface in consequence of the superjacent epidermis and dermis having been rubbed off (see p. 161). The suspensorium is always hyostylic.

The shoulder girdle and pectoral fin skeleton presents great variation, but on the whole inclines to the Teleostean type of structure. In the *Chondrostei* and in *Amia* the pectoral girdle is cartilaginous. In the other orders it is ossified very much as in Teleosts.

In the *Chondrostei* and *Crossopterygii* there are three separate membrane bones in relation with the shoulder-girdle, the supra-clavicle, clavicle and infra-clavicle,\* while in the other orders the infra-clavicle is absent. In the pectoral fin the skeleton of *Polypterus* is on the Elasmobranch type (rhipidostichous), in extinct Crossopterygians on the Dipnoan type (rachistichous and mesorachic). In other orders the arrangement on the whole is Teleostean.

The other anatomical characters of the Ganoids are (1) the possession of a conus arteriosus with more than one row of valves; (2) the very general presence of a gill on the hyoid arch supplied by a branch of the ventral aorta, or of a spiracle (see below); (3) the presence of an air-bladder with pneumatic duct; (4) the union of the urinary and Müllerian ducts and their opening by a median urogenital pore behind the anus; (5) the testis appears to be connected except in *Polypterus* with the kidney by a testicular network; (6) a spiral valve is present in the intestine (small in *Lepidosteus* and *Amia*); (7) the optic nerves form a chiasma; (8) the openings of the nasal pits are double as in Teleosteans; (9) the processus falciformis and choroid glands are absent in *Polypterus*, *Lepidosteus*, and possibly in other Ganoids; (10) the scales are bony plates embedded in the dermis, and frequently covered by a layer of peculiar substance called ganoin. Ganoin is probably vitro-dentin: it used to be

\* These bones are now often called supracleithrum, cleithrum and clavicle respectively, on the view that the last-named alone is homologous with the clavicle in the Amphibia and Amniota, the cleithral elements not being represented in these groups.

regarded as enamel. These scales in the young state and sometimes throughout life bear spines which project through the epidermis and are formed of dentine capped by enamel (*Polypterus*, *Lepidosteus*). (11) The fins frequently, not always, possess a single or double row of spine-like scales, called *fulcra*, on their anterior edge (absent in *Polypterus*, *Polyodon* and *Amia*). The dermatrichia are soft and segmented, and the pelvic fins are abdominal. (12) They lay relatively small eggs which undergo complete cleavage, and the young are hatched out as larvae which differ in many respects from the adult and possess a pronephros as in Teleosteans. In *Lepidosteus* the medullary canal arises as a solid keel-like projection of the ectoderm which subsequently becomes hollow.

The brain is on the whole Teleostean-like. There is a thin pallium (Fig. 91) and a valvula cerebelli and the cerebrum is undivided; though it

may be grooved externally so as to suggest a division into two lobes.

The branchial apparatus presents remarkable variation. In *Spatularia* (*Planirostra edentula*) there is no hyoid gill, but a pseudobranch in the spiracle as in *Acipenser*. In *Polypterus* there is no hyoid gill, nor spiracular pseudobranch. The spiracle is present in *Acipenser*, *Polyodon* and *Polypterus*, but absent in *Scaphirhynchus*, *Lepidosteus* and *Amia*. The following table summarizes the matter :—

Hyoid gill, pseudobranch and spiracle . . . *Acipenser*.

Hyoid gill, pseudobranch\* but no spiracle . . . *Lepidosteus*.

\* It is doubtful if the structure identified by Müller as pseudobranch in *Lepidosteus* is really such.

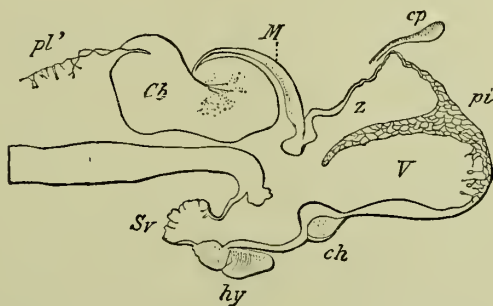


FIG. 91.—Median section through the brain of *Acipenser ruthenus* (from Gegenbaur, after Goronowitsch). *Cb* cerebellum; *ch* optic chiasma; *cp* pineal body; *hy* pituitary body; *pi* pallium with choroid plexus projecting in between the third ventricle *z* and the ventricle of the cerebrum *V*; *pl'* roof of fourth ventricle; *Sr* saccus vasculosus.



Hyoid gill, but no pseudobranch or spiracle. . . . . *Scaphirhynchus*.

Hyoid gill absent, pseudobranch and spiracle present . . . . . *Polyodon*  
(*Spatularia*).

Hyoid gill and pseudobranch absent, spiracle present . . . . . *Polypterus*.

Hyoid gill absent; pseudobranch and spiracle also absent (4 double gills) . *Amia*.

In those forms (*Polypterus* and *Polyodon*) without hyoid gill the ventral aorta still gives a branch to the hyoid arch.

Abdominal pores\* are present in all living Ganoids. Their external openings are placed on each side of the anus and they open internally into the body cavity.

Pericardio-peritoneal canals are present in the Sturgeons as single unbranched tubes; they appear to be absent in other Ganoids.

Of these characters which on the whole suggest Elasmobranch more than Teleostean affinities, it will be convenient to treat the urinogenital organs more fully at this point.

The **urinogenital** organs present many features of interest, and as they differ in important points in the different members of the group it will be necessary to describe them at some length. In all of those, the development of which is known, there is a pronephros in the larva, constructed on the Teleostean type, i.e. it consists of one large malpighian body (Fig. 92, *v*) connected by a convoluted tube (*pr.n*) with the anterior end of the longitudinal duct (*sd*) of the future kidney. In *Lepidosteus* and possibly in others, this body is connected with the peritoneal cavity by a ciliated canal (*f*). In none of them does the kidney show any differentiation into a meso- and meta-nephros, and in all the oviduct (müllerian) joins the kidney duct of its side posteriorly. Moreover müllerian ducts appear to be in all classes present, generally in both sexes, and they present the peculiarity of being short and opening into the body cavity at a point much nearer the anus than in other groups in which they are found.

We have full knowledge of the urinogenital organs in two

\* Bles, "Correlated distribution of Abdominal Pores and Nephrostomes in Fishes," *Journ. Anat. and Phys.*, 32, 1898, p. 484.

Ganoids; one of these is *Lepidosteus* of which we have a description from the pen of Balfour,\* and the other *Polypterus* in which their structure has been recently elucidated by Budgett.†

In *Lepidosteus* the kidneys extend forward from the anus about three-fifths of the length of the body cavity (Fig. 93, *k*). Anteriorly they are continuous with a band of lymphatic tissue of a very similar appearance. The ureters (*sg*), which lie on their ventral side and receive the openings of numerous collecting tubes, enlarge posteriorly, and approaching each other coalesce to form an unpaired vesicle (*bl*) which opens by a median pore

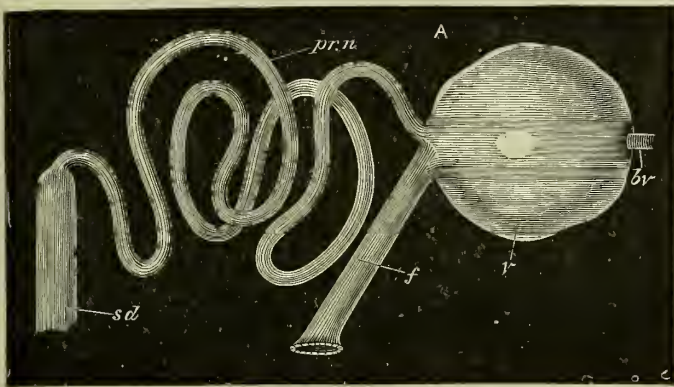


FIG. 92.—Diagrammatic view of the pronephros of *Lepidosteus* (from Balfour), isolated and seen from the side. *pr.n* Coiled tube; *sd* longitudinal duct of kidney; *v* malpighian body of pronephros; *f* tube leading from *v* to the body cavity (peritoneal funnel); *br* blood vessel of glomerulus of *v*.

on a papilla (*ug*) behind the anus. The ovary is a hollow sac, attached about its middle to the oviduct and continued backwards and forwards from this attachment into a blind process. The oviduct is a thin-walled tube, continuous in front with the ovarian sac and opening behind (*od*) into the dilated part of the kidney duct of its side. In the male the testis is lobulated and the vasa efferentia pass in the mesorchium to the kidney, where they open into a longitudinal canal. From the longitudinal canal pass off tubules which open into the kidney tubules themselves. Near the testis the vasa efferentia are united into an

\* *Phil. Trans.*, 1882.

† *Trans. Zool. Soc.*, 15, 1901, p. 323.

irregular network. No trace of the oviducts has been observed in the male.

In *Amia*\* there is a testicular network, and the posterior part of the kidney is provided with nephrostomes. In the female the oviduct opens into the body cavity.

In *Polypterus* the oviduct is short and opens anteriorly into the body cavity, and posteriorly into the kidney duct just before its union with its fellow. In the male the kidney duct dilates behind and joins its fellow to form a considerable sinus which receives the testis duct of each side and opens to the exterior behind the anus. The testis is an elongated body almost as long as the kidney, to the ventral side of which it is attached. Two parts may be distinguished in it—an anterior dilated portion which forms spermatozoa and is the functional testis, and a posterior streak-like portion—the *testis-ridge*—in which the

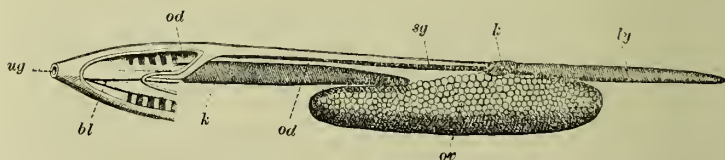


FIG. 93—Diagram of the urinogenital organs of an adult female of *Lepidosteus* (from Balfour and Parker). *od* Right oviduct; the *od* which is placed on the upper side of the figure points a little to the right of the opening of the oviduct into the dilated lower end of the kidney duct; *ov* ovary; *bl* urogenital sinus; *ug* urogenital aperture; *sg* kidney duct; the reference line goes a little too far in the figure; *k* kidney, *ly* lymphatic organ. The organs of the right side only are shown.

testicular tubules are few in number and do not form spermatozoa. The testicular tubules, both of testis and testis-ridge, open by numerous short ducts into the testis duct which is a longitudinal canal extending the whole length of the organ close to the ureter. In *Polypterus* then the testis tubules do not communicate with the kidney tubules, but there is a special testis duct which opens behind into the kidney duct at the point at which the oviduct opens in the female. No trace of oviducts has been seen in the male and there are no nephrostomes in the adult.

In the Sturgeon there is a testicular network in the male, as was first shown by Rathke, and there are short müllerian ducts in both sexes opening widely into the body cavity and behind into the kidney duct. In the female the müllerian duct is of course the oviduct. Open müllerian ducts have been seen in both sexes of *Scaphirhynchus* and *Polyodon*, but a testicular network has not yet been seen in those genera.

\* Jungersen, *Zool. Anzeiger*, 23, 1900, p. 328.

The Ganoids reached their greatest development in the Palaeozoic, Triassic and Jurassic periods. From the Cretaceous epoch onwards they have gradually become less numerous, until at the present day they are represented by a few widely scattered, extremely isolated, and for the most freshwater genera. The Ganoids are here divided into four orders—*Chondrostei*, *Crossopterygii*, *Lepidostei* and *Amioidei*.

#### Order 1. CHONDROSTEI.

*Endo-skeleton largely cartilaginous; head covered with bony plates. Body naked or with rows of bony plates, or with rhomboid, rarely cycloid scales. Operculum weakly developed, branchiostegals numerous, few, or absent; teeth small or absent. Infra-clavicle present. Caudal fin usually heterocercal. One dorsal and one anal fin, with fulcra. Paired fins non-lobate. Pelvic fins with a series of basal cartilages. Lower Devonian to present time.*

So far as the facts which can be made out from a study of the extinct forms are concerned, this order agrees with the Crossopterygians in the feebleness of the ossification round the notochordal sheath (except *Polypterus*), and in the presence of infra-clavicles; it differs from them in the absence or absorption into the body of the basal lobe of the paired fins, in the heterocercal tail, and in the absence of jugular plates between the rami of the mandible.

There are two living families, the *Acipenseridae* and the *Spatulariidae*. The following remarks apply to them:—

The tail is heterocercal. The notochord is persistent and un-constricted. Its sheath is thick, unsegmented, and entirely within the *elastica externa*. The neural and haemal arches are segmented (except in front) and placed upon the sheath, but are not continuous with one another round it (fig. 94). There are intercalated pieces both in the dorsal and ventral arches, and there is a longitudinal ligament on the neural arches. The haemal arches of the two sides meet ventrally and enclose the dorsal aorta. In addition they carry lateral projections which must be regarded as the transverse processes. These meet ventrally in the tail to enclose the caudal vein, so that in the caudal region there are two canals, one for the dorsal aorta and a ventral one for the caudal vein. The anterior part of the column is continuous with the skull, and here the neural and haemal arches are not

segmented. The notochord is continued into the base of the skull to the pituitary fossa in *Polyodon*, but not in *Acipenser*.

In the *Acipenseridae* there are five rows of large scales with projecting spines, \* one dorso-median and two on each side (Fig. 96). Between these are numerous small scale-like plates, which frequently carry one or more spines. In the caudal region these smaller plates, also carrying spines, are rhombic, in contact, and regularly arranged. In *Polyodon* (*Spatularia*), which is often described as naked, there are also small spine-bearing scale-like structures. The scales are placed in the sub-cutaneous tissue and are composed of bone (with bone corpuscles and branched processes, and in the larger scales haversian canals).

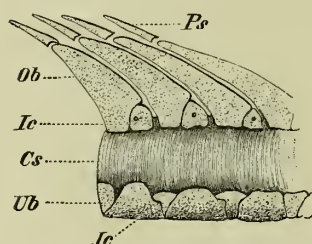


FIG. 94.—Lateral view of the vertebral column of *Spatularia* (from Wiedersheim). *Cs* sheath of notochord; *Ic* intercalated piece; *Ob* neural arch; *Ub* haemal arch; *Ps* neural spine.

The spines are composed of a similar substance in layers, either with bone cells in their lower portions or without them. There is no enamel and apparently no ganoin.

The cranium† is massive and largely cartilaginous, there being but slight traces of ossification (in the periotic region). As in other Ganoids and in Teleostei the inner wall of the otic capsule is not developed. The roof con-

sists of almost continuous cartilage, but the fontanelles though not conspicuous are not altogether absent. It is completely covered by membrane bones which lie in the dermis. There is a large parasphenoid and a single or paired vomer in the floor.

There is a partially ossified hyomandibular and a symplectic cartilage (Fig. 95) which suspend the mandibular arch. The anterior ends of the pterygoids meet in a symphysis. The visceral arches are partially ossified but the meckelian cartilages are unossified. The hyomandibular carries an opercular plate and the hyoid arch a branchiostegal ray. Membrane bones (a

\* H. Klaatsch, *Morph. Jahrb.*, 16, 1890, p. 146. O. Hertwig, *ibid.*, 2, 1876, p. 373.

† Bridge, *Osteology of Polyodon. Phil. Trans.* 1878, p. 683.



maxilla and dentary) are developed in connection with the jaws. Teeth are entirely absent in the adult, but small teeth are present in the young *Polyodon* and possibly other genera. There are five branchial arches.

In the unpaired fins the fin rays (dermotrichia) are more numerous than the interspinous supports (somactids), and the caudal fin has fulcra in a single row. The pectoral arch is unossified and the two halves are not united ventrally. They are covered by membrane bones; supra-clavicles, clavicles, and infra-clavicles being present. The pelvic arch is absent, its place being taken by enlarged basal cartilages of the fins as in Teleostei. The paired fins are without a basal lobe (non-lobate), their whole free portion being supported by dermal fin-rays. These are carried by a row of cartilages of which the posterior is possibly

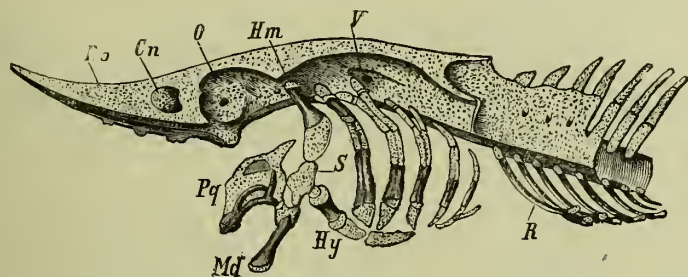


FIG. 95.—Cephalic skeleton of the sturgeon (from Claus after Wiedersheim). Ro Rostrum; Cn nasal pit; O orbit; Hm hyomandibular; S symplectic; Pq palatoquadrate; Md lower jaw; Hy hyoid; V foramen for *vagus*; R ribs.

a basal somactid (metapterygium) and the others peripheral somactids which have become articulated to the pectoral arch. The anterior dermal fin-ray is enlarged and directly articulates with the pectoral girdle.

The branchial apparatus presents remarkable variability. In *Acipenser* there is a spiracle with a pseudobranch, and a hyoid demibranch; in *Scaphirhynchus* there is no spiracle or pseudobranch, but a hyoid demibranch is present. In *Polyodon* spiracle and pseudobranch are present, but there is no hyoid gill. Each of the first four branchial arches carries a double row of gill-filaments and there is a cleft behind the fourth gill arch. In *Acipenser* the inter-branchial septa are fairly broad. In the conus there are three longitudinal rows of valves with three or four valves in each row.

Fam. 1. **Acipenseridae**. Sturgeons. With five rows of keeled plates in the skin, elongated snout, small mouth without teeth, with four barbels in front of the mouth, opercular and four double gills. Stomach without blind sac. With fulcra on the dorsal lobe of the caudal fin. Dorsal and anal fin with two rows of supports (axonosts and baseosts). Large fishes in the seas and rivers of the northern hemisphere, feeding on small animals and plants. Most are migratory (anadromous). Caviare is the ovary of the sturgeon. *Acipenser* L. with spiracle. *Scaphirhynchus* Heckel, without spiracles. Fossil remains rare; an Eocene species (*A. toliapicus* Ag.) is known, and isolated remains of scales from the Upper Lias of Whitby (*Gyrosteus*) and from the Upper Chalk of Kent (*Pholidurus*).

Fam. 2. **Spatulariidae**. Skin with small isolated scales, tail scaled as in sturgeons, snout prolonged into a thin flat blade; without barbels; with spiracle, without hyoid gill; gills, 4; gill-rakers long, in a double series on each arch, except on the fifth, which has only one series. Air-bladder cellular. Jaws with fine teeth in young individuals. Fresh-

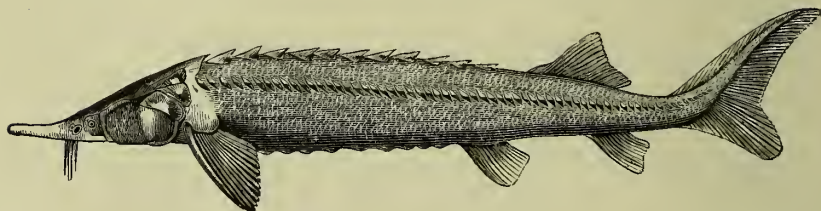


FIG. 96.—*Acipenser ruthenus* (after Heckel and Kner).

waters of N. America and China. *Polyodon* Lac., Mississippi; *Psephurus* Günther, Chinese rivers; a fossil genus *Crossopholis* Cope, from the Eocene of Wyoming.

#### EXTINCT FAMILIES.

Fam. 1. **Chondrostelidae**. Parietals and frontals paired; near the parietal a great squamosal. Jaw edentulous. Branchiostegal rays present. Operculum small, sub-operculum large. Body naked; the dorsal lobe of the caudal fin with fulcra and covered with rhombic ganoid scales. *Chondrosteus* Egerton, Lower Lias, England.

Fam. 2. **Belonorhynchidae**. Trias, Lias, may be placed here.

Fam. 3. **Palaeoniscidae**. Body elongated with rhombic, rarely cycloid scales; with operculum, sub-operculum and branchiostegal rays. In no single genus are the osteological characters well known. Devonian to Jurassic. *Cheirolepis* Ag., Devonian; *Palaeoniscus* Blv., Upper Permian; *Coccolepis* Ag., Jurassic.

Fam. 4. **Platysomidae**. Deep-bodied fishes from the Carboniferous to the Permian; very similar to the *Palaeoniscidae*. *Cheirodus* McCoy, *Eurynotus* Ag., *Platysomus* Ag., *Benedenius* Traquair.

The **Catopteridae**, Triassic, may be placed here.

## Order 2. CROSSOPTERYGII.\*

Vertebral column ossified, or unossified. Tail diphycercal or hetero-diphycercal (upper lobe of caudal fin weaker than the lower lobe, Fig. 103). Paired fins with scaled basal lobe which is either pointed or rounded. In the former case it is unibasal, rachiostichous and mesorachic, in the latter case, found only in living forms, the pectoral fin is tribasal and rhipidostichous. In place of the branchiostegal rays are two large jugular plates between the rami of the lower jaw, near which there are in many palaeozoic forms a number of smaller lateral plates and a median anterior plate. Ganoid scales, rhombic or cycloid, cover the whole body and tail. Dorsal fin either two in number; or if single, long or multifid. Devonian to present time.

This order which was established by Huxley† in 1861, is mainly based on the form of the fin, which is fringed with dermotrichia on both sides. It is difficult to state any other characters peculiar to the living and extinct forms, unless it be the two jugular plates between the rami of the lower jaw.

The following remarks apply to the living *Polypteridae* :—

The scales of *Polypterus* are very similar to those of *Lepidosteus* (see p. 177). They are

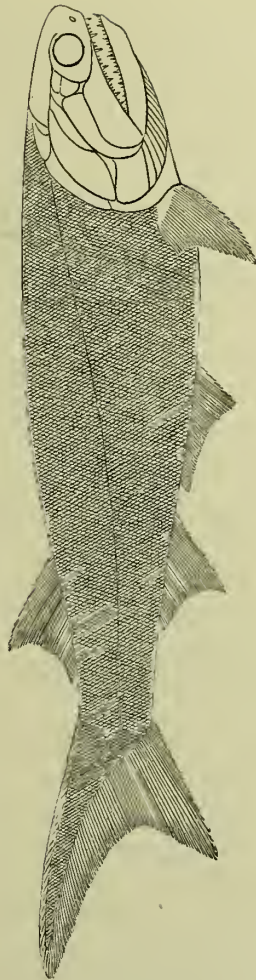


FIG. 97.—*Cheirolepis trailli*: restored (except margin of fins) by Traquair (from Smith-Woodward), quarter natural size.

\* Traquair, Cranial Osteology of *Polypterus*, *Journ. Anat. and Physiology*, 4, 1871. Pollard, "Anatomy of *Polypterus*," *Zool. Jahrb.*, 5, 1892.

† Preliminary Essay upon the systematic arrangement of the fishes of the Devonian Epoch, *Mem. Geol. Survey United Kingdom*, 1861.

attached to one another in much the same way and are arranged in oblique rows. They are rhombic in form and similarly covered by ganoin. The canals in the deeper part of them, containing blood vessels, open on the surface, but differ from those of *Lepidosteus* in being branched. They are without spines and the remains of spines, except at the bases and on the hinder surface of the pectoral fins and on the plates overlying the shoulder girdle. They are covered by soft skin in the adult, but this is frequently rubbed off in preserved specimens, leading to the view that the scales are freely exposed in the adult.

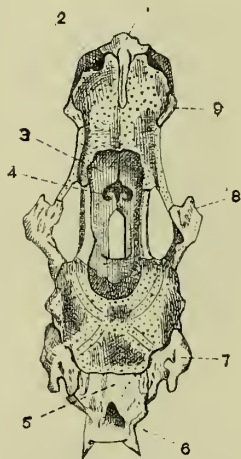


FIG. 98.—Dorsal view of the cartilaginous cranium of *Polypterus* with the membrane bones removed (after Traquair). 1 Ethmoid, 2 nasal opening, 3 sphenoid, 4 optic foramen, 5 occipital bone, 6 foramen magnum, 7 opisthotic, 8 post-frontal, 9 pre-frontal.

The vertebral column is completely ossified; the vertebrae are amphicoelous, as in Teleosteans, and carry in the body two pairs of ribs, of which the shorter and ventral pass between the muscles and the peritoneum and correspond to the ribs of other forms, while the dorsal and larger pair lie between the dorsal and ventral lateral muscles. The body of the first vertebra is united to the skull, but the arch and ribs are separate. The cranium consists mainly of persistent cartilage (Fig. 98) with a large fontanelle in the roof and in the floor (pituitary) and a few cartilage bones, of which the most important are exoccipitals which completely surround the foramen magnum, opisthotic (7),

sphenoid (? sphenethmoid), postfrontal (8), prefrontal (9) and a median ethmoid (1). There is a slender arcade of cartilage passing forward from the postfrontal to the anterior part of the sphenoid cartilage.

The whole is invested dorsally by membrane bones, while ventrally there is a parasphenoid which extends back beneath the body of the first vertebra, and two vomers (as in *Lepidosteus*). The mandibular arch is very like that of Teleosteans: in the upper jaw arcade (Fig. 100) are palatine, ectopterygoid,



entopterygoid, metapterygoid and quadrate; the lower jaw has an articular and mento-meckelian cartilage bone and an angular, splenial and dentary, the two latter being dentigerous. On the upper jaw are premaxillae, maxillae and jugals (two). The hyomandibular is ossified and bent; there is no symplectic. There is an operculum, suboperculum and a large bone called preoperculum. There are also circumorbital bones and pre- and post-spiracular bones (Fig. 99), as well as two bones (12)—the spiracular bones—in the flap which covers up the spiracle.

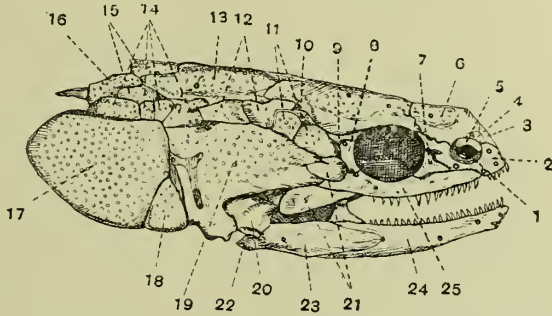


FIG. 99.—Side view of skull of *Polypterus* with membrane bones (after Traquair). 1 Nasal opening, 2 premaxilla, 3 ethmoid, 4 accessory nasal, 5 os terminale, 6 nasal, 7 anterior suborbital, 8 posterior suborbital, 9 postfrontal, 10 frontal, 11 prespiracular, 12 spiracular bones, 13 parietal, 14 post-spiracular, 15 supra-temporal, 16 post-temporal, 17 operculum, 18 sub-operculum, 19 preoperculum, 20 quadrate, 21 jugals, 22 articular, 23 angular, 24 dentary, 25 maxilla.

There are also three supra-temporals (15) and a post-temporal (16) on each side. The membrane bones are in the skin and their outer surfaces are smooth and tuberculated, and not exposed in uninjured specimens. The premaxillae and maxillae bear teeth, and the vomers, pterygoid and parasphenoid are covered with fine closely set teeth.

There are also three supra-temporals (15) and a post-temporal (16) on each side. The membrane bones are in the skin and their outer surfaces are smooth and tuberculated, and not exposed in

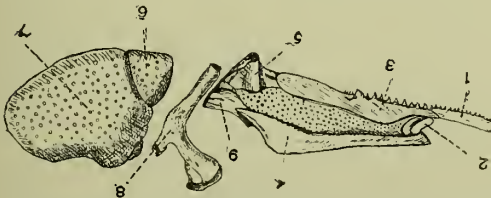


FIG. 100.—Side view of palatoquadrate, hyomandibular and opercular bones of *Polypterus* (after Traquair). 1 vomer, 2 palatine (small and not appearing in palate), 3 ectopterygoid, 4 entopterygoid, 5 quadrate, 6 suboperculum, 7 operculum, 8 hyomandibular, 9 metapterygoid.

The cartilaginous shoulder girdle is small and contains a scapular and coracoid ossification; it is overlaid by a series of clavicular bones, of which the supraclavicle is attached to the post-temporal;



there is an infraclavicle (clavicle, see note, p. 162). The skeleton

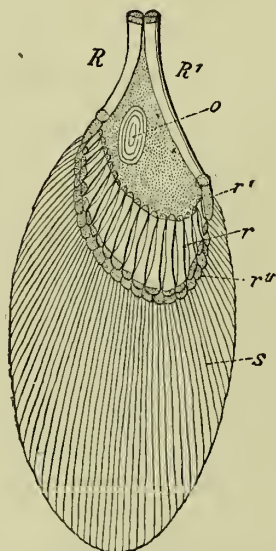


FIG. 101.—Skeleton of pectoral fin of *Polypterus* (from Gegenbaur). *R* propterygium, *R'* metapterygium; *o* ossification in mesopterygium; *r*, *r'*, *r''* primary radials (basal somactids); *r''* secondary radials; *s* fin rays.

of the pectoral fin is tribasal as in Elasmobranchs; it consists of three basal somactids, carrying two rows of peripheral somactids (*r*, *r''*) to which the dermatrichia are attached (Fig. 101). The pro- and metapterygium are ossified, the mesopterygium is mainly cartilaginous but contains an ossification (*o*).

The pelvic girdle is represented by a small piece of cartilage (Fig. 102) to which the large ossified basal somactid is attached. The latter carries a row of ossified peripheral somactids to which the dermatrichia are attached. There are no fulcra. There is a number of dorsal fins in *Polypterus*, each with an anterior spine; and the tail is diphycercal.

In *Polypterus* there are three main longitudinal rows of valves



FIG. 102. — Pelvic girdle *p* and skeleton of pelvic fin of *Polypterus* (from Gegenbaur, after v. Davidoff). *b* basal somactid; *r* peripheral somactids; *p* trace of pelvic girdle.

in the conus arteriosus with nine valves in each row, and between these there are three incomplete rows of smaller valves (about forty-five in all). Both ductus Cuvieri open into the auricle. The spiracle is present, but the hyoid gill and pseudobranch are absent. The ventral aorta sends off a branch to the hyoid arch which supplies the external gill of the larva. The fourth branchial arch bears only one row of filaments and has no slit behind it. The stomach has a caecum and there is one pyloric appendage. The air bladder is double and cellular and its duct opens into the ventral wall of the pharynx; its blood supply is from the last efferent branchial vessel and its vein joins the hepatic. According to Budgett *Polypterus* is capable of

breathing air. The pituitary body retains its opening into the buccal cavity through life.\* The young *Polypterus* has an external gill, which is attached to the operculum.

*Classification of Crossopterygii, living and extinct.*

Sub-order 1. **OSTEOLEPIDA.**

Notochord more or less persistent. Pectoral fins rounded or pointed, unibasal. Nares on the lower surface of snout.

Fam. 1. **Tarrasiidae.** Axonosts and baseosts of median fins in simple regular series, much fewer in number than the dermatrichia. *Tarrasius* Traquair, Calciferous Sandstones (Lower Carboniferous) of Dumfriesshire.

Fam. 2. **Holoptychiidae.** Body covered with overlapping cycloid ganoid scales; vertebral column unossified; pectoral fin with long pointed scaled axis (mesorachic); tail hetero-diphycercal. Axonosts of each of the dorsal and anal fins fused into a single piece with a broad distal end, bearing three to six rod-like baseosts, which are much fewer than and overlapped by the dermatrichia in all the median fins. Lateral jugular

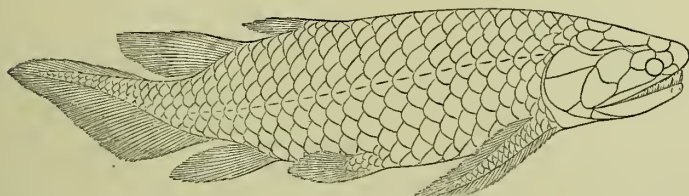


FIG. 103.—*Holoptychius flemingi*, Devonian, Scotland, after restoration by Traquair, from Woodward.

plates, clavicles and infra-clavicles present; the teeth have a complicated folded structure. *Holoptychius* Ag. (*Glyptolepis*, *Platygnathus* Ag.) Devonian; isolated teeth have been described as *Dendrodus*, *Lamnodus*, *Apedodus*.

Fam. 3. **Rhizodontidae.** Like the preceding but with shorter pectoral and pelvic fins. Devonian, Carboniferous. *Rhizodus*, *Strepsodus* *Rhizodopsis*, etc.

Fam. 4. **Osteolepididae.** Ring vertebrae in the caudal region, Devonian. *Osteolepis*, *Thursius*, *Diplopterus*, *Megalichthys*.

Fam. 5. **Onychodontidae**, known only by fragments from the Devonian, is placed here.

Fam. 6. **Coelacanthidae.** Notochord persistent, vertebral column unossified. Axonosts of each of the dorsal and anal fins fused into a single piece; a series of axonosts, equal in number to the neural and haemal spines present in the caudal fin above and below, each axonost directly connected with a single dermal fin ray. Caudal fin diphycercal; air-bladder with ossified walls; paired fins with short, obtuse axis; only one opercular bone. Lower Carboniferous to the Upper Chalk. *Coelacanthus* Ag., *Undina* Münt., *Macropoma* Ag., etc.

\* Bickford, *Anat. Anz.*, 10, 1895.

## Sub-order 2. CLADISTIA.

Notochord more or less constricted and replaced by ossified vertebrae. Baseosts in median fins rudimentary or absent; axonosts of dorsal fins equal in number to the apposed dermatrichia. Pectoral fins di- or tri-basal. Nares on the upper surface of the snout.

Fam. 7. **Polypteridae.** Body covered with rhombic ganoid scales; vertebral column ossified; tail diphyccercal; pectoral fins tribasal; two jugular plates only; dorsal fins numerous; pulp cavity of teeth simple. *Polypterus* Geoffr. (Fig. 104), with pelvic fins, rivers of North and Equatorial West Africa; *Calamoichthys* Smith, elongated and without pelvic fins, rivers of Old Calabar and the Cameroons.

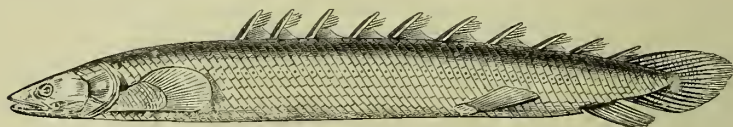


FIG. 104.—*Polypterus bichir* (from Claus).

## Order 3. LEPIDOSTEI.

Body covered with rhombic or rhomboidal scales arranged in oblique rows and articulated together. Caudal fin hemi-heterocercal. Vertebral column in the most different degrees of ossification. Unpaired, and sometimes paired fins with fulcra. Branchiostegal rays numerous, and often a median jugular plate. Always four opercular bones; between preoperculum and orbit at least one row of postorbitals. Infraclavicle absent. Somactids of the unpaired fins as numerous as the dermatrichia. Teeth pointed or conical. The pelvic fins are without baseosts.

This order, which appears to be closely allied to the *Palaeoniscidae* on the one hand and to the *Amioidei* on the other, includes the living genus *Lepidosteus*. With the exception of the Permian genus *Acentrophorus*, the extinct members are found in the Lias, Jurassic, Lower Cretaceous, and Tertiaries.

The following remarks apply to the living *Lepidosteidae*. The body is covered by rhombic scales articulated together (see p. 177). The tail is hemi-heterocercal. The paired fins are non-lobate, and all the fins bear paired fulcra. The jaws are much elongated, forming a snout; the premaxillae form most of the upper jaw. Both jaws bear teeth, small and large, and there are fine close-set teeth on the palatines and vomers. The vertebrae are well developed and ossified, and have opisthocelous centra. The chondrocranium is large and cartilaginous with

embedded cartilage bones much as in the salmon, and is completely invested by membrane bones. The vomer is double. There is a symplectic in the suspensorium, several bony elements are present in the mandible, and the maxilla is divided transversely into many bones.

The pectoral girdle is as in Teleosteans, with scapula and coracoid ossifications and overlying clavicle. The pectoral fin has one row of basal elements carrying the dermatrichia. The pelvic girdle is absent.

In *Lepidosteus* \* the scales of the trunk are arranged in oblique rows which pass from above and in front backwards and ventrally. The scales of a row are more closely connected with each other than with those of neighbouring rows, in consequence of a peg and socket articulation. Each scale has its anterior and dorsal angle produced into a process which fits into an excavation under the next dorsal scale of the same row, where it is attached by a ligamentous band. The centre of the scale is bored by one or several canals which pass right through it and transmit blood vessels. The scale consists in its deeper portions of

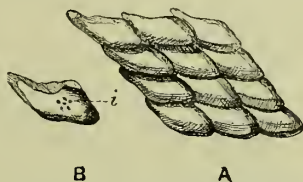


FIG. 105.—A portion of the armour of *Lepidosteus*; B single scale showing antero-dorsal process which fits below the next dorsal scale (after O. Hertwig); *i* foramina for blood vessels.

bone with bone corpuscles and vertically directed fibres, which are prolongations of large scleroblast cells at the surface (so-called odontoblasts, they do not become enclosed) and of a superficial layer of structureless dentine or ganoin, as it was called by Williamson, which is only found on the exposed part of the scale, and was formerly taken for enamel. In some parts of the body (ventral side of head, investing bones of skull and shoulder girdle, the fin scales) the scales carry one or a number of small teeth, which consist of enamel, dentine with fibres, and a pulp-cavity. In the young animal all the scales carry teeth, with the dentine of which the ganoin of the scale is continuous. The scales are developed as plates in the dermis,

\* O. Hertwig and Klaatsch, *op. cit.*; see also W. C. Williamson, On the microscop. structure of scales, etc., of fishes, *Phil. Trans.*, 1849 and 1851. Nickerson, Scales of *Lepidosteus*, *Bull. Mus. Comp. Zoology, Harvard*, 24, 1893.



the scleroblasts of which become successively included in the scale to form the bone corpuscles. The ganoin is formed later (in a fish of fifty-two months) by the cells on the upper surface of the plate. The teeth are developed as in Selachians on a papilla of dermis projecting into the epidermis. The cells of the papilla form the dentine and those of the epidermis the small cap of enamel. Some of the scales possess processes which indicate where teeth were formerly attached.

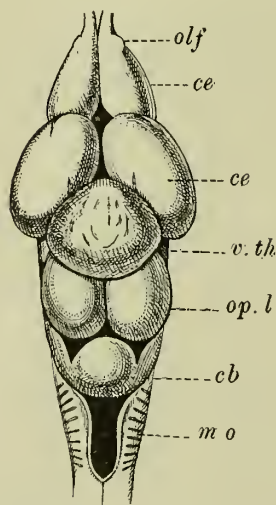


FIG. 106.—Dorsal view of the brain of *Lepidosteus* (after Balfour and Parker). *cb* cerebellum; *ce, ce* anterior and posterior lobe of cerebellum; *m o* medulla oblongata; *olf* olfactory lobes; *op. l* optic lobes; *v. th* vesicle of thalamencephalon.

There is no spiracle in the embryo or adult, though there is a pouch-like trace of one in the embryo; but the hyoid bears a gill, dorsal to which is a structure called by J. Müller the pseudobranch. This so-called pseudobranch is not found in the larva. There are four double gills, and a cleft behind the fourth branchial arch.

The conus arteriosus possesses eight\* equally developed longitudinal rows of valves, five in each row. The ventral aorta gives off on each side posteriorly two branches, one to the third and fourth branchial arches, and one to the second; anteriorly it also gives off two, the posterior of which goes to the first branchial and the anterior to the hyoid.

The so-called pseudobranch appears to be supplied by arterial blood from the efferent vessel of the first branchial arch, as in other fishes. The left ductus Cuvieri opens into the sinus, the right into the auricle. The stomach is without a blind sac and there is a number of pyloric caeca and a small but distinct pancreas. The intestine is coiled and has a spiral valve pos-

\* Boas states, *Morph. Jahrb.* 6, p. 323, that the valves of four of these rows are smaller than those of the other four. There seems to be some variation in the valves of the conus of Ganoids.



teriorly. The air-bladder is single and opens into the pharynx dorsally. It has a continuous central cavity opening on each side into lateral chambers which are placed in the thickness of the wall.

In *Lepidosteus* the cerebrum (Fig. 106) is divided into two parts, an anterior and a posterior. The anterior part tapers in front into the olfactory lobes and is double; the posterior part is single and its ventricle possesses a thin roof like that of the thalamencephalon, with which it is continuous. The dorsal part of its side walls, where they pass into the roof are everted and thickened and form the prominent posterior cerebral lobes (Fig. 106). The anterior part of the roof of the thalamencephalon is produced dorsalwards into a large thin-walled vesicle which projects just in front of the pineal body. The cerebellum is of medium size and has a forwardly projecting lobe.

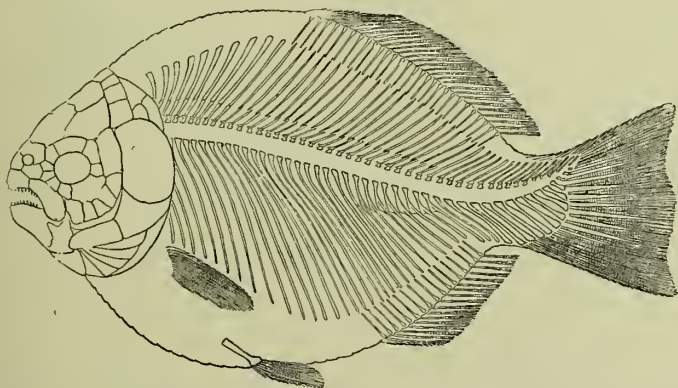


FIG. 107.—*Dapedius politus*, restored with scales removed, quarter natural size, Lower Lias (from British Museum Catalogue).

Fam. 1. **Lepidosteidae.** Body covered with thick, rhombic, ganoid scales, vertebral column completely ossified, vertebrae opisthocoelous; tail heterocercal; the snout is much elongated. *Lepidosteus* Lac., gar-pikes. Fresh-waters of N. America and Cuba, one species is known from China. Sluggish habit, voracious, valueless as food.

#### *Extinct families.*

Fam. 1. **Stylodontidae.** All fins with fulcra. Jaws and vomer with several rows of teeth. Vertebral column composed of half vertebrae or of ring-vertebrae. Upper Permian to Cretaceous. *Acentrophorus* Traquair, *Semionotus* Ag., *Dapedius* de la Beche, a deep-bodied fish (Fig. 107).

Fam. 2. **Sphaerodontidae**. Very similar to preceding; with obtusely conical or chisel-shaped teeth. Trias to Chalk. *Colobodus* Ag., *Lepidotus* Ag. (Fig. 108).

Fam. 3. **Eugnathidae**. Very similar to preceding; elongated bodies; caudal fin homocercal or hemi-heterocercal; Trias to Cretaceous. *Eugnathus* Ag., *Ptycholepis* Ag., *Caturus* Ag., *Strobilodus* Way.

Fam. 4. **Macrosemiidae**. *Macrosemius* Ag., *Ophiopsis* Ag., *Propterus* Ag., *Notagodus* Ag.

Fam. 5. **Pholidophoridae**. *Pholidopleurus* Bronn.

Fam. 6. **Pycnodontidae**. Body laterally compressed, high, oval; covered by rhomboidal scales, articulated together and strengthened by a vertical ridge; scales sometimes absent in the caudal region, rarely absent altogether. Notochord persistent, without ossifications in its sheath, but ribs, arches and spinous processes ossified. Caudal fin internally hemi-heterocercal; fulcra absent; pelvis small, anal and dorsal long; fulcra absent; somactids of the unpaired fins equal in number to

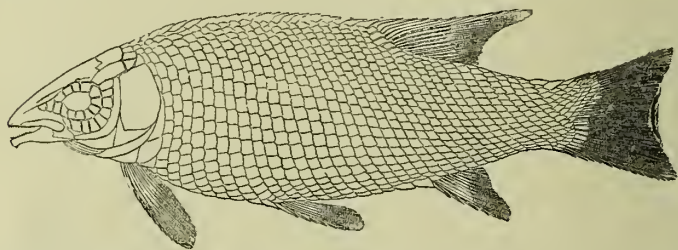


FIG. 108.—*Lepidotus minor*, restored, one-fifth natural size, Purbeck Beds (from British Museum Catalogue).]

the segmented dermatotrichia; opercular apparatus reduced, often only one opercular bone present. Dentition of oval, crushing teeth. The chondrocranium often well ossified. Infraclavicles absent. Jurassic, Cretaceous, Eocene. *Gyrodus* Ag., *Mesturus* Wagn., *Mesodon* Wagn. (Fig. 109), *Pycnodus* Ag., etc.

Fam. 7. **Aspidorhynchidae**. Very similar to preceding, but with ring-shaped or complete and biconcave vertebrae (pleurocentra and hypocentra never distinct). Caudal fin homocercal; snout elongated and pointed; scales rhomboidal, unequal; lower jaw with movable premandibular; fulcra weak. Lower Oolite to Upper Chalk. *Aspidorhynchus* Ag., *Belonostomus* Ag.

Fam. 8. **Lepidosteidae**. See p. 179.

#### Order 4. AMIOIDEI.

Body covered with thin cycloid or rhombic scales, overlapping, but not articulating, without ganoin. Caudal fin internally heterocercal, externally symmetrical (hemi-heterocercal). Vertebral column with either half-vertebrae or completely ossified amphicoelous vertebrae, or without vertebrae, ossification extending from

the arches into the notochordal sheath. *Fulcræ* present or absent. *Branchiostegal* rays flattened; a median jugular plate. *Teeth* pointed, conical. *From the Lias onwards.*

This order, which is close to the *Lepidostei*, contains the single living genus *Amia*. It approaches more closely to the *Teleostei* than any other ganoid fish, but it differs from them

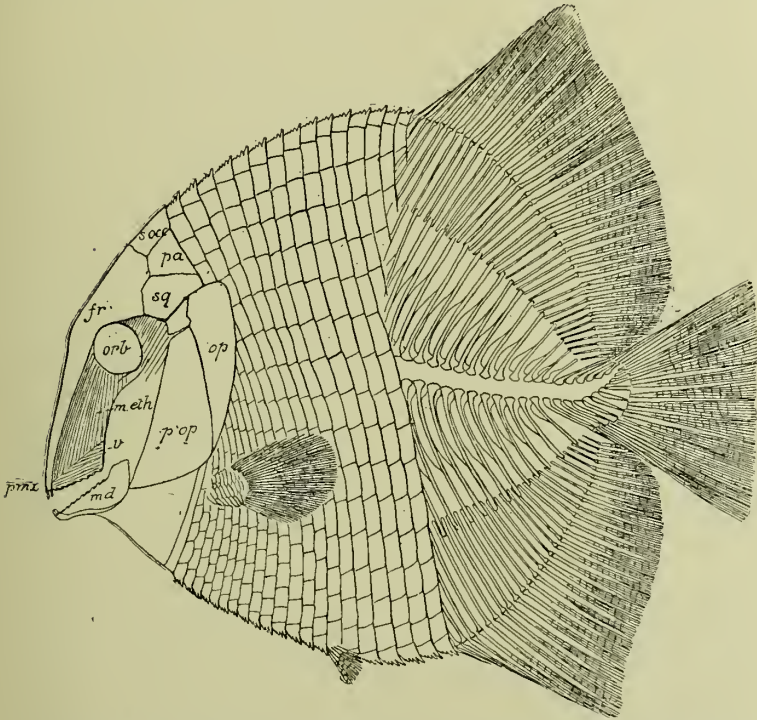


FIG. 109.—*Mesodon macropterus*, restored, with cheek-plates removed, two-thirds natural size, Upper Jurassic (after Smith Woodward). *fr* frontal, *meth* mesethmoid, *md* mandible, *op* operculum, *orb* orbit, *p.op* preoperculum, *pa* parietal, *pmx* premaxilla, *soc* supraoccipital, *sq* squamosal, *v* vomer. (The caudal region is destitute of scales in this fish.)

in important features of the urinogenital organs and structure of the heart, and alimentary canal.

Fam. 1. **Pachycormidae.** Extinct. Ethmoid region more or less produced in front of the mouth; vertebral column variable as in the order. *Fulcræ* present, branchiostegal rays numerous. *Lias* to Lower Cretaceous. *Pachycormus* Ag., *Euthynotus* Wagn., *Hypsocormus* Wagn.

Fam. 2. **Amiidae.** Vertebral column ossified with complete amphicoelous vertebrae. The caudal region consisting of vertically divided

half-vertebrae, of which one half (variously described as the anterior and posterior) carries the arches. Fulcra absent. Tail somewhat heterocercal, more so in the young.

The scales of *Amia*, which are thin, elastic and cycloidal, consist of a superficial layer containing bone corpuscles, and a deeper layer containing fibres. They thus closely resemble the scales of *Teleostei*, and are without a superficial layer of ganoin (Klaatsch, *op. cit.*, p. 179).

The skull\* is decidedly Teleostean in its structure. The chondrocranium is well developed and contains a few widely separate cartilage bones. As in *Lepidosteus*, it is without fenestrae in the roof. From the fact that two neural arches are attached to the basioccipital bone, it would appear that the centra of the two first vertebrae are fused to the skull. The investing bones of the dorsal surface, though closely applied to the cartilage, are dermal structures, and are for the most part not covered externally by soft skin in the adult. The vomer is double and bears teeth. The suspensorial apparatus is almost exactly similar to that typical of Teleosteans. The premaxillae, maxillae, palatines, and pterygoids also bear teeth. There are four opercular bones, numerous branchiostegal rays, and a median jugular plate. The shoulder girdle is cartilaginous and is overlaid by the large clavicle. It carries one basal cartilage (metapterygium), to one side of which the somactids, which carry the dermatrichia, are attached. Spiracle, pseudobranch and hyoid gill are absent. There are four double gills and a slit behind the fourth arch. The conus arteriosus has three transverse rows of valves with four or five valves in each row. The base of the ventral aorta is slightly swollen into a kind of bulbus. The air-bladder is cellular and lung-like and opens by a duct into the dorsal wall of the pharynx. Stomach with a blind sac, pyloric caeca absent. The intestine contains a spiral valve. For urinogenital organs, see p. 166. A single living genus *Amia* L., with one species, in the freshwaters of the United States; flesh valueless as food; species are known in the Lower Tertiaries of Europe and N. America. *Megalurus* Ag., with fulcra, from the Upper Jurassic may be placed here.

Fam. 3. **Oligopleuridae.** Upper Jurassic to Upper Cretaceous. *Oenoscopus* Costa, *Spathiurus* Davis.

\* Bridge, Cranial Osteology of *Amia calva*, *Journ. Anat. and Phys.*, xi., 1877, p. 605.

## CHAPTER VIII.

### SUB-CLASS (AND ORDER) TELEOSTEI.\*

*Fishes with a bony endoskeleton, distinct, usually amphicoelous, vertebrae, a supraoccipital bone, pectinate gills, a branchial operculum and usually a hyoidean pseudobranch. Without spiracle, conus arteriosus, optic chiasma, and intestinal spiral valve. An air-bladder is often present. The gonads are usually continuous with their ducts, and the testes are not connected with the kidney. The eggs are heavily yolked, but usually small, and the young are, with a few exceptions, hatched in an immature condition and undergo a larval development.*

The *Teleostei* include the vast majority of living fishes. They are found in freshwater as well as in the sea, and in some cases they possess organs which enable them to exist in or to breathe air (*Anabas*, *Periophthalmus*, fishes which live in foul or muddy water, e.g. many marsh fishes).

The form of the body is exceedingly variable, most often it is typically piscine, but it may be elongated and snake-like as in the eels, strongly compressed laterally in the ribbon-fishes (*Trichiurus*, etc.) and in the flat-fishes (*Pleuronectidae*), or the vertical axis may equal or even exceed the longitudinal in length (*Orthogoriscus*). The tail which is usually the principal organ of locomotion is in the last-named modification so much reduced that it appears to be absent, and in the sea-horses (*Hippocampus*) it is without caudal fin and is used as a prehensile organ.

The body is divided into head, trunk, and tail; the gill-opening usually marks the boundary between the head and

\* See, besides the works of J. Müller, Günther, Day, Jordan and Evermann, Boulenger, Bridge, already cited, G. B. Goode and T. H. Bean, "Oceanic Ichthyology," *Memoirs of the Museum of Comparative Anatomy at Harvard College*, 22, 1896.



trunk, and the vent that between the trunk and tail. The mouth is usually at the anterior end of the head, but it varies considerably in form and position; it may be anterior or superior (on the upper surface), or inferior or lateral (extending along each side of the head). The upper jaw may be formed by the premaxillaries (intermaxillaries) and maxillaries or by the premaxillaries only, and both jaws may be provided with tactile appendages called *barbels*. The nostrils are usually double on each side, and in a few cases (some eels) the anterior or lower opening perforates the upper lip. The eyes are large, are usually without lids, and the cornea is flat. In cave-fishes and in abyssal forms they may be much reduced and even hidden beneath the skin, but in some deep-sea forms they are enormously enlarged. The branchial slits are hidden by the gill-cover, which is a fold of skin, containing dorsally four flat bones, the opercular bones or opercles, and ventrally a number of bony rods called the branchiostegal rays. The branchial aperture or aperture of the space bounded by the operculum is usually a slit of considerable dorso-ventral extent, but in some cases it is much restricted, and in *Symbranchus*, the openings of the two sides coalesce in the middle line. The space on the throat between the gill apertures is called the *isthmus*. There is no spiracle. The actual gill-openings themselves, i.e. the openings leading from the pharynx into the space below the gill-cover are not tubular but simply slits, separated by the rod-like branchial arches. These carry the gills which are usually filiform and project freely. There are usually two rows of them (*holobranchs*) on each branchial arch, projecting like the prongs of a comb; hence they are said to be pectinate (Fig. 118). There are usually five gill-slits, but the last is always smaller than the others, and is sometimes absent, in which case the fourth branchial arch bears only one row of gill-filaments (*hemibranch*). They may be still further reduced. There are five branchial arches, but the last never bears filaments. The hyoid never carries true gill-filaments, but it generally carries them in a reduced form as a *pseudobranch*. In some cases the pseudobranch is without a trace of filaments and has the form of a red glandular patch. The *vent* is usually at the junction of the trunk and tail, but it may be shifted far back on the tail or far forward on the trunk. It consists of at least two openings placed close together, the foremost being the anus

and the hinder one the urinogenital aperture. The genital aperture may, however, in some forms be separate from and in front of the urinary.

The median fins are subject to considerable variation. There are usually two dorsal fins, a caudal and an anal fin, but there may be a single dorsal fin continuous round the tail with the anal, or there may be a series of finlets in place of the dorsal fin, and the anal may be multiple or absent. The paired fins are in two pairs, the *pectoral* and *pelvic* (sometimes called *ventral*). Of these the pelvics are small, vary considerably in position and are sometimes absent (fishes which live in mud); they may be behind the pectoral on the abdominal surface in which case they are said to be *abdominal* in position, or they may be below the pectorals (*thoracic*) or in front of them (*jugal*). In some cases they coalesce and form a suctorial organ (*Gobies*) and in some Blennies they are adapted for walking. The pectorals are usually close behind the gill-opening and vary much in size. They assist the fish in balancing and enable it to execute backward movements. In some forms (*Periophthalmus*, *Trigla*, *Lophius*, etc.) the pectoral fins are used for walking, and in the flying fish (*Exocoetus*) they are enlarged to form parachute-like organs. All the fins are supported by osseous fin-rays (dermotrichia) which are for the most part jointed and flexible (sometimes they branch peripherally), but in some cases (Acanthopterygian fishes) more or fewer of the anterior dermatrichia in the dorsal (anterior dorsal if there are two), anal, and pelvic fins are unjointed and generally stiffened. Such dermatrichia are called spines. The caudal dermatrichia are always jointed, as are all the dermatrichia in the Malacopterygian fishes. In some Malacopterygian fishes the posterior dorsal fin is without jointed dermatrichia, but contains adipose tissue only and delicate unjointed horny dermatrichia resembling the embryonic dermatrichia (actinotrichia): this is the *adipose* fin of certain *Siluridae*, *Salmonidae*, etc. The dermatrichia of the ventral part of the caudal fin are carried by the haemal arches, those of the other unpaired fins by special skeletal rods—the somactids (p. 54)—lying in the median fibrous septum separating the dorsal parts of the muscles. These somactids of the Teleostean unpaired fin are often called *interspinous bones*.

The spines of the dorsal fin of Acanthopterygians can be raised or depressed at will. In the depressed position the spines may cover one another completely (*homacanth*), or they may be turned slightly to one side or the other alternately (*heteracanth*).

The skin usually contains pigment and may be very brightly coloured. Many fishes possess the power of changing their colour in a protective manner according to their surroundings, and in almost all the dorsal surface is darker in colour than the ventral. The body is usually covered with scales, overlapping one another in such a way that the posterior part of the scale is free and covers the anterior part of the next scale behind. The scales are thin plates of bone imbedded in the dermis, and are more frequently absent from the head and fins than elsewhere. They are absent in most eels and in fishes with electric organs. The epidermis is soft and contains many mucous and pigment cells.

The scales have a concentric striation and are of two kinds, *cycloid* and *ctenoid*. In ctenoid scales the posterior free margin possesses denticulations which may extend on to the surface, whereas in cycloid scales such denticulations are absent. In some cases the scales are enlarged into great scutes (*Siluridae*, *Lophobranchii*, *Plectognathi*) and in *Balistidae* they have the form of ossified papillae which project in a shagreen-like manner. In *Siluridae* the scales may carry movably articulated dermal teeth.

The scales of most Teleostean fishes are thin calcified lamellae, without bone corpuscles, lying in a dermal sac. They are surrounded by scleroblasts which, as in *Lepidosteus*, form them and add to them during growth. The outer portion of the scales is structureless, the inner contains fibres. In some forms, scleroblasts of the upper surface are included and become bone corpuscles, so that the scales consist of an outer part showing ordinary bone structure and an inner consisting of connective tissue impregnated with calcareous matter by the scleroblasts.

The spines which are present on the scales of some *Teleostei*, e.g. some Acanthopterygians and Plectognaths, frequently contain a cavity which suggests a pulp cavity. They may possibly be regarded as homologous with the spines of Elasmobranchs, but without the enamel cap. The spines of the hinder part of the ctenoid scales are due to the sculpture of the surface and are not denticles.

According to the recent and as yet (March 1904) unpublished researches of Marett Tims, the scales of *Gadus* consist of a number of small plates of structureless bone (vitrodentine) lying close together on a fibrous basis. In the young state each plate carries a small spine which does not reach the epidermis.

The sense organs \* (nerve eminences) of the lateral line are

\* F. Leydig, Integument u. Hautsinnesorgane der Knochenfische, *Zool. Jahrb. Anat.*, 8, 1894, p. 1-152. W. Collinge, Sensory Canal System of Teleostei, *Proc. Zool. Soc.*, 1895, pp. 274-299. R. McDonnell, Lateral line in Fishes, *Trans. R. Irish Acad.*, 129, 1862, pp. 161-187.

usually enclosed in canals, but they may be unenclosed and only protected by flaps of skin (*Batrachus*, *Lophius*, etc). Their distribution, whether they are enclosed or not, resembles that found in Elasmobranchs and is indicated on Fig. 42. When they are enclosed in canals, the tubes which leave the canal and open on the surface are simple, ending in a single external pore ; or they branch considerably before reaching the surface and open by several pores. The trunk part of the lateral line canal is placed in the dermis and is usually without osseous supports, but on the head the canals are either enclosed in small bones which lie outside the skull bones, or they burrow in and are protected by the bones of the skull and visceral arches themselves. There may be accessory lateral lines in the trunk, placed on the sides of the body near the dorsal and ventral middle lines. There are no ampullary canals.

Many deep-sea fishes possess numerous shining bodies in the skin resembling in their general features eyes.\* It appears probable that they are phosphorescent organs. They are found either on the head near the eyes, on the lower jaw, at the end of barbels, under the gill-cover, or in rows in which they may be segmentally arranged along the sides of the body, and sometimes in connection with the lateral line. They vary considerably in structure from being simply glandular patches of the skin which are supposed to secrete a phosphorescent mucus to a state in which they are more eyelike in appearance and possess a lens-like body which, it is suggested, acts like the lens of a bull's-eye lantern in concentrating the rays proceeding from the internal parts of the organ. In the latter case a kind of tapetum can often be made out at the back of the organ which appears to act as a reflector. They are probably in all cases modified skin glands. It appears probable that in many cases these organs are for the purpose of enabling their possessors, which are generally provided with large eyes, to see in the dark abysses of the ocean, but in some cases no doubt they act as lures (when placed at the end of barbels or far back on the body). In the case of *Ipnops* in which

\* F. Leydig, *Die augenähnlichen Organe der Fische*. Bonn, 1881. M. Ussow, Ueber d. Bau der sogenannten augenähnlichen Flecken etc., *Bull. Soc. Nat. de Moscou*, 1879. A. Günther, Deep-Sea Fishes, in *Challenger Reports*, 22, 1887, and appendices by H. N. Moseley and R. v. Lendenfeld.



there is no trace of eyes, optic nerve or olfactory nerve, and in which the supposed luminous organs have the form of two broad laminae on the upper surface of the head, and in other deep sea forms in which the eyes are imperfect (e.g. the *Pediculati*) they can only be of use as lures.

In the endoskeleton the primitive cartilage is largely replaced by bone, but some cartilage, varying in amount in the different forms, may persist.

The vertebral column is usually completely ossified and consists of amphicoelous vertebrae (Fig. 34). The vertebrae are connected by articulating processes placed on the neural arches. In the trunk the centra carry transverse processes, which are directed outwards, and ribs which are articulated to the centra or to the base of the transverse processes (Fig. 34). In the tail the centra carry complete haemal arches, which enclose a canal containing the caudal artery and vein and are prolonged like the neural arches into a median spine. In some forms a pair of small bony rods—the inter-muscular bones, are attached to the centra near the neural arches.

The vertebrae are arcicentrous, the notochordal sheath remaining thin, but the skeletogenous tissue develops very little cartilage being rapidly replaced by membrane bone in the centra as well as in the arches.

In most Teleosteans the end of the vertebral column is bent dorsalwards, and is unsegmented, though the notochordal sheath is ossified to form a bony urostyle. The haemal arches of this part of the vertebral column persist in a modified form as the hypural bones, which carry the dermatrichia of the ventral part of the caudal fin (p. 55). In such cases the tail though symmetrical externally, is internally asymmetrical, and is said to be *homocercal* (see pp. 55, 56). In a few forms (*Gadidae*, etc.), the end of the vertebral column is not bent dorsalwards, and the tail-fin is symmetrical internally as well as externally (diphycercal). In these fishes the dermatrichia of the ventral part of the caudal fin are carried by interspinous bones, and it seems highly probable that the true tail-fin has atrophied completely, as it has in some *Heteromi*, *Syngnathidae*, etc., in which the tail tapers to a point and is without any trace of a caudal fin, and has been secondarily replaced by a backward extension of the dorsal and anal fins (p. 55). Such tails are therefore secondarily diphycercal.



The skull is always hyostylic and possesses both membrane and cartilage bones. It differs considerably in the extent to which the primitive cartilage persists. In many forms, e.g. the salmon, pike (particularly in the less specialised, more ganoid-like fishes), a considerable amount of cartilage persists and the cartilage bones are separated

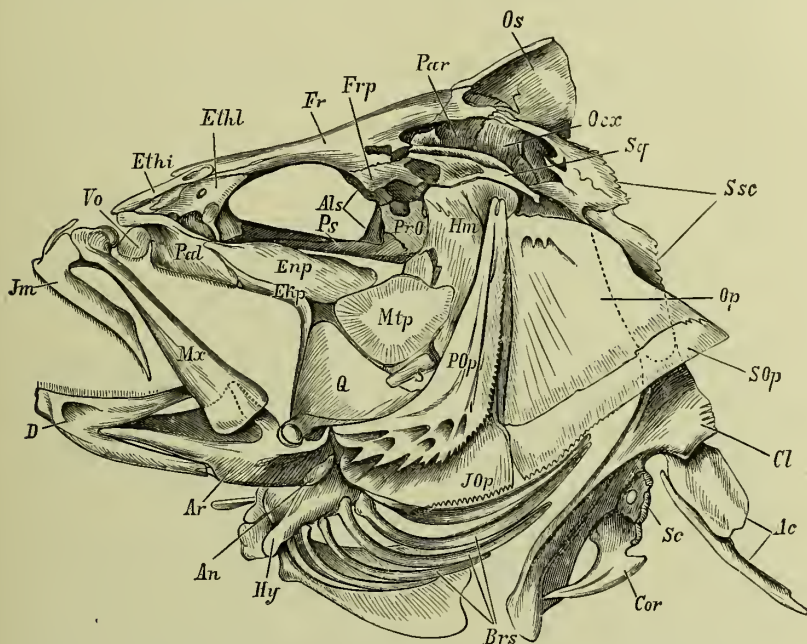


FIG. 110.—Cephalic skeleton of *Perca fluviatilis* (Règne animal). *Ac* post-clavicles; *Als* alisphenoid; *An* angular; *Ar* articular; *Brs* branchio-stegal rays; *Cl* clavicle; *Cor* coracoid; *D* dentary; *Ekp* ectopterygoid; *Enp* entopterygoid; *Ethl* median ethmoid; *Ethl* lateral ethmoid (prefrontal); *Fr* frontal; *Frp* postfrontal (sphenotic); *Hm* hyomandibular; *Hy* hyoid arch; *Jm* premaxilla; *JOp* interoperculum; *Mtp* metapterygoid; *Mx* maxilla; *Oex* epiotic; *Op* operculum; *Os* supraoccipital; *Pal* palatine; *Par* parietal; *P0p* preoperculum; *PrO* prootic; *Ps* parasphenoid; *Q* quadrate; *S* symplectic; *Sc* scapula; *SOp* suboperculum; *Sq* pterotic; *Ssc* supraclavicle; *Vo* vomer.

by wide tracts of intervening cartilage. In others, e.g. the cod, the cartilage is almost entirely ossified. The cartilage is usually deficient in the roof of the skull except in the occipital region, in which a basi-, two ex- and a supra-occipital are developed. The auditory region usually presents five separate cartilage bones, the epiotic, opisthotic, prootic, the pterotic and the sphenotic (postfrontal). The sphenoid region is feebly ossified: there is always a small basisphenoid and sometimes an alisphenoid

and orbitosphenoid, and the anterior part of it generally acquires a considerable vertical extension forming an interorbital septum (absent in Siluroids, Cyprinoids, etc.). The ethmoid region remains unossified, or at most has two bones—the lateral ethmoids or prefrontals (Fig. 110 *Ethl*). The membrane bones of the roof are parietals (*Par*), large frontals (*Fr*) and a bone over the ethmoid (supraethmoidal or median ethmoid, *Ethi*). There may be other bones, called nasals, over the ethmoidal region. The parietals may touch in the middle line between the frontals and supraoccipital, or be pushed apart and separated by the junction of the frontals and the supraoccipital. In the floor there is a large and important parasphenoid strengthening the base of the skull and a vomer (*Vo*) underlying the ethmoid region. The orbit is surrounded by a ring of circumorbital membrane bones (not shown in Fig. 110), of which the anterior is called the lacrymal. Premaxillae (*Jm*) and maxillae (*Mx*) are present, and there may be a jugal, but the maxillae are usually toothless and frequently take no part in the formation of the edge of the mouth. The palatine bar of the mandibular arch always presents osseous palatine, pterygoid and quadrate elements: in front is the palatine (*Pal*) often dentigerous; then follows the pterygoid region usually presenting three elements—the pterygoid (ectopterygoid), the mesopterygoid (entopterygoid *Enp*) and the metapterygoid (*Mtp*); lastly comes the quadrate (*Q*) which gives articulation to the lower jaw. The front (palatine) end of this bar is attached to the ethmoid region, while the quadrate is not attached to the cranium directly, but is supported by the strong dorsal element (hyomandibular) of the hyoid arch. In the lower jaws Meckel's cartilage persists, being ossified proximally as the articular (*Ar*), and ensheathed by the dentary bone (*D*) distally: in addition there is often an angular element (*An*). In the hyoid arch there is a powerful dorsal hyomandibular element which presents two bones, the hyomandibular (*Hm*) and the symplectic (*S*). The hyomandibular bone articulates with the auditory region of the cranium and passes ventralwards behind the metapterygoid, while the symplectic lies distally and is closely applied to the quadrate. The rest of the hyoid arch consists of three ossified pieces on each side (Fig. 111)—the epihyal (*c*), ceratohyal (*b*) and hypohyal. The

epihyal is joined to the cartilage interval in the hyomandibular element between the hyomandibular and the symplectic bones by a small osseous piece the interhyal (*d*), while ventrally the hypohyal joins the large median, sometimes toothed glossohyal. In connection with the hyoid arch is a number of membrane bones—the opercular bones supporting the operculum, and the branchiostegal rays in the branchiostegal membrane. The opercular bones are in connection with the dorsal, hyomandibular element and consist of the operculum (Fig. 110, *Op*) and preoperculum (*POp*), and sometimes of a suboperculum

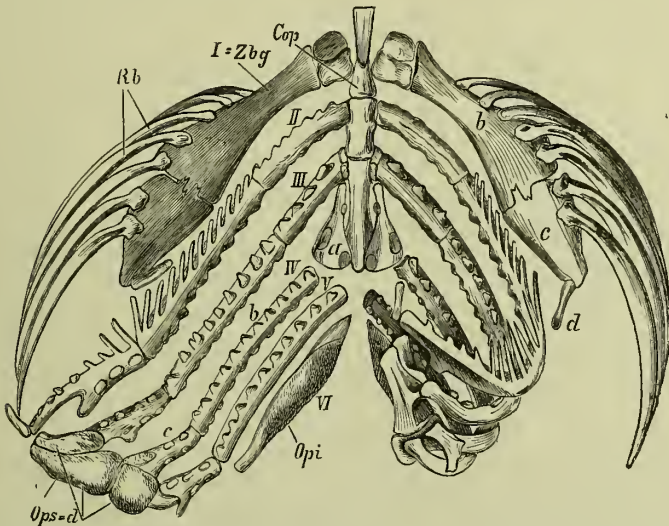


FIG. 111. Hyoid apparatus and branchial arches of *Perca fluviatilis* (Règne animal). *a*, *b*, *c*, *d* segments of the branchial arches; the upper joints *Ops* are the superior pharyngeal bones (pharyngobranchials); *VI*, *Opi* the inferior pharyngeal bones (reduced fifth branchials); *Cop* median pieces (copulae); *Rb* branchiostegal rays; *I = Zbg* hyoid arch; *II—V* branchial arches.

(*SOp*) and interoperculum (*JOp*). The branchiostegal rays (*Brs*) are attached to the lower part of the hyoid arch, partly to the inner and partly to the outer side (Fig. 111 *Rb*). There are five pairs of branchial arches. Of these the anterior four are usually segmented into four pieces (Fig 111), the pharyngo- (*Ops=d*), epi- (*c*), cerato- (*b*) and hypo- (*a*) branchials. More or fewer of the pharyngo-branchials, which are not joined to the skull or vertebral column, are united with one another to form the so-called *superior pharyngeal bone* which generally bears

teeth (*Ops*). The hypobranchials, which may be wanting in the fourth arch, are attached to a varying number of median elements, the *copulae* or basibranchials (*Cop*). The fifth branchial arch is reduced to a single rod on each side which is usually strongly toothed, and the pair are called the *inferior pharyngeal bones* (*Opi*); they are sometimes ankylosed to form a single bone. The four anterior branchial arches bear small tooth-like projections, in one or two rows, which act as strainers; these are the gill-rakers.

Pectoral and pelvic\* paired fins are present, but one or both of them may be absent.

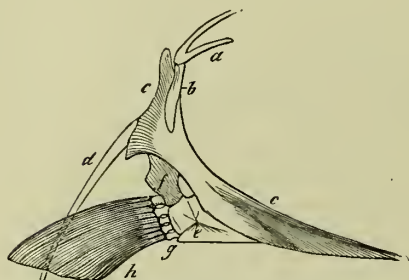


FIG. 112.—Right pectoral girdle and fin of *Gadus* (after Gegenbaur). *c* clavicle (cleithrum); *b* supraclavicle (supracleithrum); *a* post-temporal; *d* post-clavicle; *f* scapula; *e* coracoid; *g* basal somactids of the fin; *h* bony dermotrichia.

In the pectoral girdle, which is usually present even when the fin is absent, the primitive cartilaginous coraco-scapular elements are but slightly developed and relatively unimportant, while the membrane bones (clavicles †) are largely developed.

The coraco-scapular arches do not join ventrally and are attached to the inner sides of the clavicles. They present two bony elements—the scapula and coracoid (by some regarded as precoracoid) with persistent intervening cartilage. The scapula usually has a foramen, and there is sometimes a third bony element placed dorsal to the coracoid and in front of the scapula and called the mesocoracoid. The clavicle (cleithrum) is a large membrane bone meeting its fellow ventrally under the throat. To its dorsal end there is usually attached a smaller supraclavicle (supracleithrum) which is connected dorsally with a forked bone the post-temporal. This bone is attached to the auditory region of the skull, by one prong to the epiotic and by the other to the pterotic bone. Projecting back from the

\* The pelvic paired fins are usually called *ventrals*.

† Called *cleithra* by some anatomists, on the view that they are not homologous with the clavicles of higher Vertebrates (see notes, p. 162).



upper end of the clavicle is a bony rod, the post-clavicle. There is no infraclavicle. The skeleton of the fin consists of usually five basal ossified somactids which are articulated with the coraco-scapula, and of a row of small cartilaginous pieces representing distal somactids. These are followed by the dermatrichia, the anterior of which is continuous with the anterior of the basal somactids.

The pelvic girdle is always absent, its place being taken by a large osseous basal somactid, commonly called the basipterygium; to this are attached a few small, partly bony, distal somactids, which carry the dermatrichia.

The brain \* of Teleosteans presents the following features.

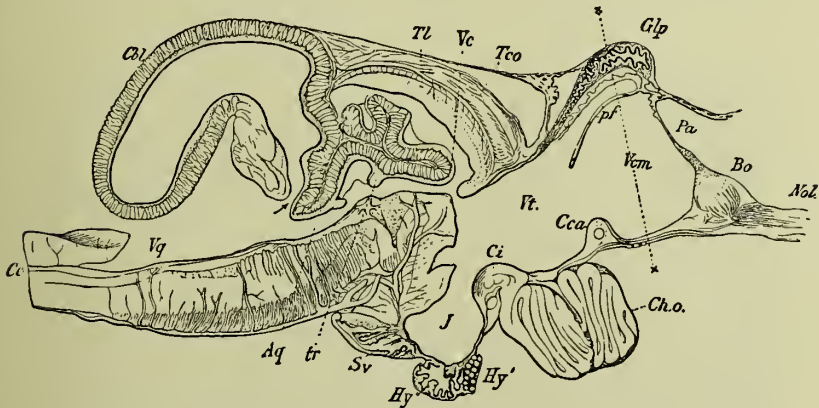


FIG. 113.—Median longitudinal vertical section through the brain of the trout (from Gegenbaur, after Rabl-Rückhard). *Aq* aqueductus sylvii; *Bo* olfactory lobe; *Cbl* cerebellum; *Cc* central canal of spinal cord; *Cca* anterior commissure; *Cho.* optic nerves; *Ci* inferior commissure; *Glp* pineal body; *Hy, Hy'* hypophysis; *J* infundibulum; *Nolz* olfactory nerve; *Pa* pallium; *pf* velum transversum; *Sv* sacculus vasculosus; *Tco* pia mater on the dorsal side of the mid-brain; *Tl* dorsal wall of mid-brain between the two optic lobes; *tr* crossing of the fibres of the fourth nerve; *Vc* valvula cerebelli; *Vem* ventricle of the cerebrum; *Vq* fourth ventricle; *Vt* third ventricle.

(1) The olfactory lobes are usually much elongated and slender; they are swollen at their free ends against the nasal capsules and at their origin. The cerebral ventricle is continued into the swollen base.†

\* Rabl-Rückhard, *Das Grosshirn der Knochenfische*, etc., *Arch. f. Anat. und Phys., Anat. Abt.*, 1883, p. 279–322. E. Baudelot, *Recherches sur le système nerveux des Poissons*, Paris, 1883. A. Schafer, *Die morphol. u. hist. Entwick. d. Kleinhirns der Teleostei*, *Morph. Jahrb.*, 21.

† There seems to be some difference of opinion as to whether these basal swellings alone constitute the olfactory lobes, the slender prolongations being only olfactory nerves. It has been suggested that in some fishes, e.g. Salmon, this is the case, whereas in others, e.g. Cyprinoids, the whole elongated structure is also part of the olfactory lobe.



(2) The cerebrum is not clearly marked off from the thalamencephalon, and its roof is entirely composed of a thin *pallium*. The latero-ventral parts are thickened into the great corpora striata, which were formerly taken for the cerebral hemispheres themselves. The ventricle of the cerebrum is entirely undivided, and the pallium or dorsal wall of it is not marked by a groove (Fig. 114).

(3) The thalamencephalon is very inconspicuous and the optic thalami are hardly if at all developed. The anterior part of the thin roof is folded inwards in the usual way (Fig. 113 *pf.*). The pineal body lies in the skull over the pallium; it has folded walls and appears to open by a narrow pore at its point of attachment to the roof just in front of the posterior commissure. There is no parietal organ. The floor presents the usual structure; in front is the thickening caused by the optic nerves, which simply cross after leaving the brain and do not form a chiasma. The infundibulum possesses lateral lobi inferiores, and is provided posteriorly with a glandular sac, the saccus vasculosus, opening into it by a minute pore. The pituitary body is solid and is attached to the infundibulum in front

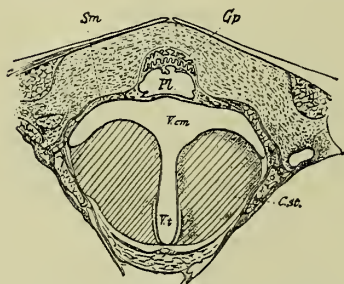


FIG. 114.—Transverse section through the cerebrum of the trout, through the line *xx* in Fig. 113. *Vcm* and *Vt* Ventricle of the cerebrum; *Cst* corpus striatum; *Sm* pallium; *Gp* pineal body; *Pl* choroid plexus (after Rabl-Rückhard from Gegenbaur).

of the saccus vasculosus.

(4) The mid-brain presents the two optic lobes (corpora bigemina) dorsally and contains a projection formed by the wall of the brain at the junction of the optic lobes and cerebellum. This is the *valvula cerebelli* (*Vc*), or fornix of Gottsche.

(5) The hind-brain is in the usual form, the cerebellum being large and containing a prolongation of the fourth ventricle. It projects back over the medulla oblongata. In some Teleosteans (e.g. *Gymnarchus*, *Mormyridae*) the brain attains a very large size, the cerebellum and sometimes the optic lobes being especially well developed.

The spinal cord frequently ends in an oval or spherical swelling. In some forms (*Plectognathi*) it is much reduced in length;

e.g. in *Orthogoriscus mola* it is barely as long as the brain and hardly reaches beyond the skull. In such cases it ends in a slender filum terminale.

The central canal usually contains a fibre \* (Reissner's fibre), which extends from the anterior end of the optic lobes, with which it is continuous, backwards along the whole length of the central canal. It consists of a bundle of nerve fibres, and communicates with the tissues of the spinal cord throughout its course. It appears to be absent in blind fishes.

In some Teleosteans (*Ctenolabrus*, *Pleuronectes*, etc.) giant nerve cells † are found in the posterior fissure of the spinal cord, their neurites passing into the substance of the cord.

The cranial nerves ‡ resemble in their general arrangement those of other fishes.

The ramus ophthalmicus profundus if present is much reduced. There is a dorsal branch of the fifth nerve—the *ramus lateralis accessorius* or *r. recurrens trigemini*—which receiving branches from the facial and vagus passes dorsally in the cranium to perforate the frontal bone. It then travels backwards near the skin to supply the skin of the trunk near the dorsal fin (sense-buds and pit-organs). It appears to be composed partly of so-called *communis* (afferent-visceral) fibres (ramus lateralis accessorius), and partly of lateralis fibres supplying pit-organs and derived from the facial.

**Sense organs.** The olfactory organ is usually provided with two openings.

The eye is distinguished by the possession of a flat cornea and a sclerotic which is frequently more or less ossified. The lens is closely approximated to the cornea, the anterior chamber of the eye being small. Traversing the vitreous humour, somewhat on the lower side of the eyeball, and extending from the entrance of the optic nerve to the eye, is a band of tissue (a process of the choroid coat) containing blood vessels and smooth muscular fibres; this is the *processus falciformis*. At its point of attachment to the lens it is swollen into the so-called *campanula halleri*. One of the functions of this structure is said to be that it assists in accommodation for vision of distant objects,

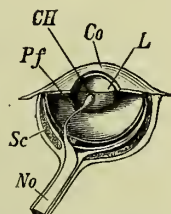


FIG. 115.—Horizontal section through the eye of *Esor lucius* (from Claus). Co cornea; L lens; Pf processus falciformis; CH campanula Halleri; No optic nerve; Se ossifications in the sclerotic.

\* Sargent, *Anat. Anzeiger*, 17, 1900, p. 33. A similar fibre has been described in *Petromyzon*.

† Sargent, *Anat. Anzeiger*, 15, 1898, p. 212.

‡ Stannius, *op. cit.* Cole, *Gadus*, *Trans. Lin. Soc.*, (2), 7. Herrick, *Menidia*, *Journ. Comp. Neurol.*, 9, 1899.

by drawing the lens nearer to the retina. The eyes of fishes when at rest are accommodated for vision of near objects, i.e. the opposite of the condition in the eyes of the terrestrial Vertebrates. There is a layer of tissue between the choroid and sclerotic which contains crystals, the *argentea*; and round the entrance of the optic nerve between the same coats there is in many Teleosts (those with a pseudobranch) a vascular plexus of unknown function, called the *choroid gland*.

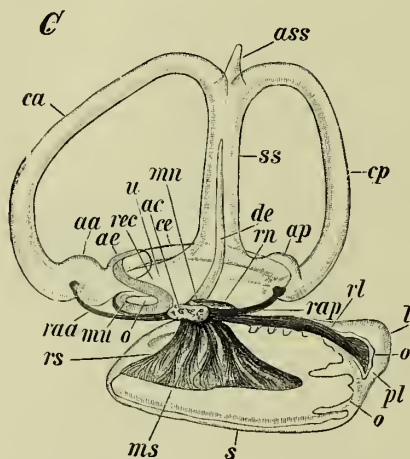


FIG. 116.—Membranous labyrinth of *Perca fluviatilis*, inner view (from Wiedersheim). aa anterior ampulla; ac auditory nerve; ae external, ap posterior ampulla; ass apex sinus superioris; ca anterior, ce horizontal, cp posterior semicircular canal; de ductus endolymphaticus; l lagena cochleaeti mn macula acustica neglecta; ms macula acusca sacculi; mu macula ac. recessus utriculi; o otoliths of the recessus utriculi, the saccule and the lagena; pl papilla acustica lagenae; raa, rap, rl, rs, nerves to the ampullae of the anterior, and posterior semicircular canals, to the lagena, and to the saccule; rec recessus utriculi; s saccule; ss sinus utriculi superior; u utricle.

The eye-muscles are the usual four recti and two obliqui; the former often arise from a suberanian bony canal the floor of which is formed by the parasphenoid. Movable eyelids are not present, though there may be a circular fold of skin round the eye. In *Anableps* the cornea is crossed by a horizontal stripe which divides the pupil, so that there appear to be two pupils one above the other.

The auditory organ\* consists of the membranous labyrinth and is without accessory structures except in those forms (*Ostariophysi*) in which a chain of small bones connects it with the air bladder (see p. 202). The membranous labyrinth is con-

tained in the auditory region of the skull wall, but the cavity in which it is placed is not shut off from the cranial cavity by bone or cartilage. It is constructed on the usual plan, consisting of a central chamber or vestibule and three semicircular canals (Fig. 116). The vestibule is divided by a constriction into two parts, an upper, the *utricle* (u) into which the semi-

\* G. Retzius, *Das Gehörorgan der Wirbelthiere*, Bd. 1., Stockholm, 1881.

circular canals open, and a lower the *sacculæ* (*s*), which possesses a small posteriorly directed process (*lagena*) representing the cochlea. The otoliths vary much in form in different fishes. They occur in the utricle, sacculæ and lagena. That in the sacculæ (the *sagitta*) is generally the largest and of a crystalline structure. There is another small one (*asteriscus*) in the lagena, and a third in the utricle close to the ampullæ of the anterior and horizontal canals (*o*). The ductus endolymphaticus is present as a process of the sacculæ, but does not open externally.

The lateral line has already been described (p. 187). Its sense organs are probably innervated by branches of the facial and lateral line branch of the vagus as in other fishes, but this has not been shown in all cases.

The alimentary canal is distinguished by the very general presence of an air bladder, which must be regarded as an appendage of the oesophagus, though it is often in the adult separate from this ; by the presence of more or less numerous appendages—the pyloric caeca, opening into the first part of the intestine ; by the inconspicuous character of the pancreas, which in some cases is even said to be absent ; by the absence of a spiral valve in the intestine ; and by the absence of a cloaca common to the alimentary canal and urinogenital organs.

The teeth \* are usually well-developed, but in some cases are altogether absent (some *Lophobranchii*, *Coregonus*). They may be borne by the maxillary, premaxillary, palatine, vomer, dentary bones, by the glosso-hyal and by the branchial arches, and rarely by the pterygoid and parasphenoid. The maxilla is usually without teeth, and does not always form part of the edge of the mouth. The teeth are generally ankylosed to the subjacent bony structures, but in some cases there is a ligamentous connection of such a kind that they can be bent inwards when food is being swallowed, but not in the reverse direction (some *Gadidae*, *Lophius*, *Esox*). In a few cases they are implanted in sockets (*Sphyræna*, etc.). As a rule teeth continue to be developed throughout life from new germs (not from pre-existing germs), placed behind the functional teeth. These come into function and position as the old teeth are worn down and cast off. When the teeth are implanted in sockets, the new tooth, though

\* R. Owen, *Odontography*, London, 1840-45. C. S. Tomes, *Dental Anatomy*, London, 1898.



developed behind the old one, comes to lie beneath it, so that the succession is vertical.

The teeth are generally conical, and may be minute, slender and sharp-pointed (*villiiform*, e.g. Perch), or longer but very fine (*ciliiform*, *setiform*, as in Chaetodonts). Larger conical teeth are termed card-like (*rasp-teeth*, *raduliform*). In Goniodonts the teeth are bent on themselves like a tenterhook. They may vary in shape in different parts of the mouth, the anterior teeth being conical, and the posterior broad and molar-like for grinding the food, as in the wolf-fish (Fig. 117), and many *Sparidae*. In *Sargus* indeed the anterior teeth are incisor-like, and in *Dentex* there are canine-like teeth. Small molar-like teeth are called *granular*.

In *Labrus* crushing teeth are borne by the upper and lower pharyngeal bones. Compound teeth, which are found in the Gymnodonts and the *Scari*,\* are made up of a number of teeth which are developed successively but are joined by cement when full grown and functional. They thus present the appearance of teeth which continue to grow throughout life.

Pharyngeal teeth may be present on the superior and inferior pharyngeal bones. In the Cyprinoids the mouth is edentulous, and teeth are only found on the inferior pharyngeal bones, which bite against a tubercle

on the basi-occipital. They are also present on the edges of the branchial arches, but except in a few cases, e.g. *Orthogoriscus*, in which they are long and sharp, these gill-teeth are little more than horny excrescences, which however are sometimes elongated into setiform horny processes—the *gill-rakers*.

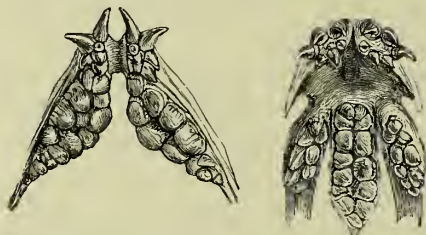


FIG. 117.—Teeth of the Wolf-fish, *Anarrhichas lupus* (after Günther).

There is usually on the floor of the mouth a small non-muscular elevation which represents the **tongue**; it is supported by the glosso-hyal, and is sometimes toothed. The oesophagus is a wide tube, hardly if at all marked off from the stomach. The stomach, which varies in form, is usually but slightly dilated and is either U-shaped as in *Elasmobranchs*, or is provided with a caecal prolongation of its cardiac portion and a short pyloric region placed near the junction with the oesophagus (Fig. 37). The intestine is usually slightly convoluted, is without a spiral valve (though a trace of one may be made out in some genera), and opens to the exterior by the anus. In some forms (e.g. *Tinca*, *Cobitis*) the striped muscles of the oesophagus are continued over the stomach and intestine outside the smooth

\* J. E. Boas, Die Zähne der Scaroiden, *Z. f. w. Z.*, 32, 1879, p. 189–215.



muscles. The pyloric caeca are tubular structures opening into the first part of the intestine just beyond the pylorus; they vary in number from one to two hundred, and are very generally present. The liver is provided with a gall bladder which opens just beyond the pylorus. It generally contains much oily matter, but in some forms the oil occurs in all the tissues of the body and is not only a feature of the liver. The pancreas,\* the presence of which in Teleostei used to be denied, is not usually a conspicuous structure, though functionally of great importance, especially in those Teleosts in which the stomach is without gastric glands. It is either embedded in the liver or diffused in the mesentery, and its duct opens in close connection with the hepatic duct. In some forms (*Salmo*, *Gadus*, *Perca*, *Platessa*, *Brama*, etc.) there is a small gland opening with the bile duct, which is possibly pancreatic.

The **Thyroid** † body is represented by small reddish masses lying ventral to the ventral aorta, and the **thymus** † is placed at the dorsal ends of the last pair of branchial arches.

**The respiratory organs.**—There is no spiracle. The branchial apertures are narrow slits and the tissue between them has the form of an arch, not of a septum. In consequence of this the gills themselves are filamentous, not lamellar (Fig. 118). The external openings of the clefts are covered by the operculum. The gill-filaments are borne in a double

row (holobranch) by the four anterior branchial arches, the last gill-aperture is smaller than the others, and the fifth branchial arch never bears gill-filaments.

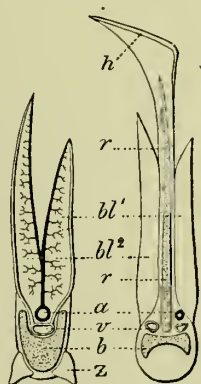


FIG. 118.—Transverse section through a branchial arch of *Zygaena* (right hand) and of *Gadus* (left) (after R. Hertwig, from Wiedersheim). *a* and *v* afferent and efferent blood vessels, *b* skeletal branchial arch, *bl'* and *bl''* posterior and anterior demibranch together constituting a holobranch, *h* septum between two branchial apertures in *Zygaena*, *r* cartilaginous branchial ray supporting the same, *z* small tooth-like tubercle (sometimes elongated as a gill-raker) in a double row on the branchial arch of *Gadus*.

E. Laguesse, Structure, etc., du pancreas d'après les travaux récents, *Journ. Anat. Phys.*, Paris, 30, 1894, p. 591 and 731. E. Goepfert, Die Entwick. d. Pancreas Teleost., *Morph. Jahrb.*, 20, 1893.

† F. Maurer, Schilddrüse u. Thymus in Teleostier, *Morph. Jahrb.*, xi., 1886, p. 128-75.

A pseudobranch \* is generally present on the posterior side of the hyoid arch. It contains a rete mirabile and usually has the form of short filaments or ridges. In some cases it is concealed below the mucous membrane, and the organ may have the form of a red, lobed swelling (so-called glandular pseudobranch or vaso-ganglion). Sometimes it lies so far from the surface that it is quite hidden: indeed it may be covered by fat and muscles and even by bone. It is sometimes absent, and its absence appears to be very generally correlated with that of the choroid gland. The function of the pseudobranch is unknown; it lies in the course of the greater part of the blood supply to the eye (see below), and it is generally regarded as a vestige of a hyoid gill.

Certain fishes, e.g. eels, can exist for some time out of water, but those with large gill-apertures usually perish rapidly. In some active fishes, e.g. the *Scombridae*, the temperature of the blood is considerably higher than that of the water; probably it is always slightly higher, but we know very little on this subject.

The Teleosts have usually five gill-clefts, but the fifth is always smaller than the rest and is sometimes absent. In this case the fourth branchial arch bears one row of filaments only (demibranch) or may be gill-less. In some forms the gill-apparatus, both arches and gills, may be still more reduced (*Symbranchidae*, *Malthe*, etc.; in *Amphipnous cuchia* the second branchial arch alone bears gill-filaments). In some *Lophobranchii* the gills have the form of curious tufted processes.

Accessory respiratory structures are met with, especially in cases in which the gill-filaments are reduced. Thus in *Amphipnous* there is a lung-like vascular-lined sac, opening into the first gill-cleft, for breathing air. In *Saccobranchus* there is a very similar sac. In *Anabas scandens*, in which the gill-apparatus is complete, the superior pharyngeal bones are honeycombed so as to form a laminated organ covered with vascular mucous membrane to enable it to breathe out of water (Fig. 38). Accessory respiratory organs are also found in the *Ophiocephalidae*, certain *Siluridae* (*Clarias*, *Heterobranchus*, *Heterotis*), and in *Chanos*.

The air-bladder is present in most but not in all Teleostei. It presents great variety of structure throughout the group. In the *Malacopterygii*, *Ostariophysi*, *Apodes*, and *Haplomi* it usually, but not always, opens into the alimentary canal (usually into the oesophagus) on its dorsal side by the *pneumatic duct* (laterally in *Erythrinus*), which may however be partly or

\* Joh. Müller, Vergl. Anat. der Myxinoiden, *loc. cit.* Maurer, *Morph. Jahrbuch*, 9, 1883, p. 229.

entirely occluded. In other *Teleostei* there is rarely \* a ductus pneumaticus in the adult, though such may be present in the young form; and the air-bladder is a closed sac. Inasmuch as it develops in the embryo as a diverticulum of the oesophagus, this closed condition must be regarded as secondary. In the *Clupeidae* the ductus pneumaticus opens into the fundus of the stomach and in the Herring there is a second duct opening to the exterior on the left side of the reproductive aperture. The air-bladder always contains gas which consists of nitrogen, oxygen and a trace of carbonic acid. It lies dorsal to the alimentary canal, and is usually closely adherent to the ventral surface of the kidneys, lying between those organs and the peritoneum, and in many Siluroids it is partly enclosed in osseous capsules formed by the vertebrae. In some cases however it projects into the body cavity, lying more or less loosely. Its walls consist of connective and elastic tissue and yield isinglass. Tufts of blood vessels in the form of *retia mirabilia* (red bodies) covered by a glandular epithelium are often present on its walls, and sometimes project into it, like huge vascular glomeruli. These vascular bodies are absent from the *Ostariophysi* and from most fishes which have a pneumatic duct. They are however present in some of the latter, e.g. the eel. The air-bladder may be coextensive in length with the body-cavity, but it frequently extends as a single or double prolongation some distance beyond into the caudal region beneath the caudal vertebrae (*Gymnotus*, *Ophiocephalus*, etc.), or forwards into (see below) or towards the head (*Gadus*, etc.). Sometimes it is much restricted (some *Siluridae*, *Pediculati*, *Plectognathi*, etc.). In some cases it is partially or completely divided transversely into two or even more compartments (*Cyprinidae*, *Characinidae*); more rarely it is divided longitudinally (*Arius*). In some forms it is so much reduced in size that it almost escapes notice (some *Siluridae* and *Cyprinidae*). It frequently gives off diverticula, which in the *Sciaenidae* and *Polynemidae* are numerous and branched. As a general rule the internal cavity is unbroken except for the partitions complete or

\* An open pneumatic duct is said to be present in *Holocentrum*, *Priacanthus*, *Caesio*, etc. See Kner, Einiges üb. die Thymus bei Fischen u. d. Schwimmblase der Stachelflosser, *Sitz. Mat. Nat. Classe Akad. Wiss.*, Wien, 49, 1864, p. 455.

incomplete just referred to, and the lining may be smooth or cellular (*Clupeidae*, etc.), but sometimes it is much broken up and has spongy, lung-like structure (*Heterotis*, *Gymnarchus*, and other forms).

In the *Ostariophysi* the anterior end of the air-bladder is connected by a chain of small bones, which are probably detached portions of some of the anterior vertebrae and are called the Weberian ossicles,\* with the wall of a chamber in the skull wall enclosing a diverticulum of the membranous labyrinth; and in other cases anterior prolongations of the air-bladder reach the skull and come into immediate contact with the wall of the space in which the membranous labyrinth is contained.

In the simplest cases (*Myripristis*, *Holocentrum*, *Sparus*, *Sargus*, etc.) the two anterior horns of the air-bladder apply themselves to membranous spaces in the bony wall of the occipital region containing the membranous labyrinth. In many *Clupeidae* the slender anterior end of the air-bladder enters a canal in the basi-occipital and divides into two narrow branches. Each of these dilates within the bone and divides again into two, each of which forms a spherical swelling. A process from the vestibule (utricle) of the membranous labyrinth comes into contact with these vesicles; moreover, the vestibules of the two sides are connected by a transverse canal. In the *Ostariophysi*, in which the connection is effected by a chain of ossicles, a few of the anterior vertebrae are ankylosed together and modified in certain of their parts, some of which are partially detached to form the auditory or Weberian ossicles. These are four in number, of which three, the tripus (malleus, Fig. 119, 11), intercalarium (incus, 9) and scaphium (stapes 8) form a chain connecting the air-bladder with the membranous labyrinth. In addition there is a fourth—the claustrum—partly dorsal to and partly in front of the scaphium, which, however does not form part of the chain, but simply lies in the wall of the atrium (see below).

The first vertebra is represented by the centrum only which is distinct from but firmly connected to the skull and the next centrum. The second centrum (10) although it shows no marked sign of being composite, consists of the completely fused centra of vertebrae 2, 3 and 4. It is therefore called the complex centrum. To the hind end of the *complex centrum* the three next centra may be united, but these remain distinguishable. The sacculus (15) of the membranous labyrinth gives off a process, the ductus endolymphaticus (4), which unites with its fellow in the middle line, and gives off posteriorly from the point of union a median sac, the *saccus endolymphaticus* (5). The sacculus and saccus lie in excavations of the basioccipital bone, called respectively the *foveae sacculi* (16) and the *cavum sinus imparis* (14). These are partly separated from one

\* E. H. Weber, *De aure et auditu hominis et animalium, Pars I., De aure animalium aquatilis*, Leipzig, 1820. T. W. Bridge and A. C. Haddon, The air-bladder and Weberian ossicles in the Siluroid Fishes, *Phil. Trans.*, 184, 1893, p. 65-333.



another and from the cranial cavity by bony plates, but they open into the cranial cavity in front. The foveae sacculi (16) end blindly behind, but the *cavum sinus imparis* opens behind into two laterally-placed chambers the floor of which is formed by the basioccipital, the sides and roof by thick fibrous walls. These chambers are the *atria sinus imparis* (13). To the outer wall of these is attached a process of the scaphium (8), the anterior of the three ossicles. Of these, the posterior or tripus (11) is by far the largest, and is inserted behind into the fibres of the anterior chamber of the air-bladder; laterally it has a process articulating with the complex centrum, and anteriorly it is connected by a strong ligament—the *interossicular ligament* (12)—to the scaphium. In this ligament and between the tripus and scaphium, is the intercalarium (9). The tripus and intercalarium are partly enclosed in a thin-walled fibrous sac, containing a delicate fibrous network and called the *saccus paravertebralis*. The air-bladder is divided into an anterior and posterior chamber, of which the anterior is usually especially distensible, and in the *Siluridae* comes into close contact with the skin on each side. The posterior division is generally divided into two by a longitudinal septum which frequently gives off incomplete transverse septa. The ductus pneumaticus opens into the anterior chamber.

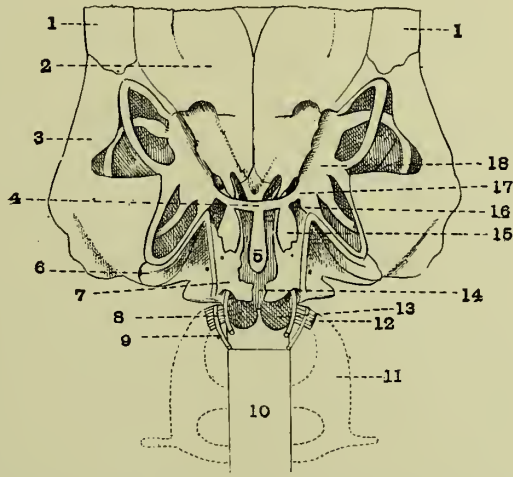


FIG. 119.—A view from above of the cranial floor and anterior vertebrae of *Macrurus acmurus*, semidiagrammatic (after Bridge and Haddon). The brain has been removed, and the bone cut away, so as to expose more completely the membranous labyrinth. 1 sphenotic, 2 prootic, 3 pterotic, 4 ductus endolymphaticus, 5 sacculus endolymphaticus, 6 epiotic, 7 exoccipital, 8 scaphium, 9 intercalarium, 10 complex centrum, 11 tripus, 12 interossicular ligament, 13 atrium sinus imparis, 14 cavum sinus imparis, 15 sacculus, 16 fovea sacculi, 17 ductus sacculo-utricularis, 18 utricle.

Striped muscles are frequently present in the wall of the air-bladder (species of *Trigla*, *Batrachus*, *Pogonias*, *Zeus*, and others). Sometimes there are extrinsic muscles passing from the ventral surface of the vertebral column on to the air-bladder (species of *Gadus*, *Diodon*, *Tetrodon*, etc.).

The blood supply of the air-bladder is arterial from the system of the dorsal aorta, either from the efferent branchial vessels, from the coeliac artery or from the dorsal aorta. In *Gym-*



*narchus* the efferent vessels of the third and fourth branchial arches go exclusively to the air bladder (Hyrtl). The veins join either the system of the posterior cardinal, or the hepatic, or the portal.

The air-bladder is extraordinarily variable in its occurrence. It is entirely absent in some families, e.g. *Blennidae*, *Pleuronectidae*, *Symbranchidae*. It may be present in some genera of a family and absent in others, or even in different species of the same genus.\*

Several functions † have been ascribed to the air-bladder ; it has been said to be hydrostatic, a resonator, sound producing, and respiratory. There can be but little doubt that it is a hydrostatic organ : ‡ its function appears to be to keep the weight of the fish equal to the weight of the volume of water it displaces. Thus if the fish sinks, its body is compressed and the specific gravity is increased. To meet this the air-bladder slowly secretes gas, which distends the bladder and so restores the specific gravity of the fish to its former point. Further, when the fish rises, its air-bladder becomes distended and its specific gravity diminishes. The fish consequently has some difficulty in preventing its body rising to the surface. To meet this, the superfluous gas is slowly absorbed and the air-bladder becomes reduced in bulk so that the specific gravity of the fish returns to its normal point. In the *Ostariophysi* the reduction of pressure causes the fish to expel the gas through its pneumatic duct, but this does not always occur in other fishes with pneumatic duct, though possibly it does so in some cases. In fishes without pneumatic duct the only way in which the superfluous gas can be removed is by absorption. With regard to the process of secretion, it takes place so slowly that it would not be worth while for a fish to change its depth unless it meant the change to be of some duration. Moreover, Biot,§ and more recently Moreau, have shown that the gas secreted is mostly oxygen. The gas in the air-bladder of fishes taken near the surface contains nitrogen, oxygen, and a trace of carbonic acid (not more than 1 or 2 per cent.). The nitrogen in such cases is

\* See Stannius, *Handbuch*, 2nd edit. *loc. cit.*, p. 221.

† Vide W. Sorensen, in *Journal of Anatomy and Physiology*, 29, 1895, p. 109, *et seq.*

‡ A. Moreau, *Recherches exp. s. l. fonctions de la vessie natatoire*, *Ann. d. Sci. Nat.*, 4, 1876.

§ *Mémoires d. l. Société d'Arcueil*, 1, 1807.

considerably in excess of the oxygen, which amounts to from 9 to 20 per cent. In fishes taken from deeper water the percentage of oxygen increases, to as much as 87 to 90 per cent. in fishes taken from a great depth. Further, if the air-bladder be artificially emptied, the fish sinks to the bottom, but it slowly recovers by gas-secretion; the gas so secreted is richer in oxygen than air. At the same time nitrogen must also be secreted, and sometimes appears to be the only gas secreted.\* Recently Bohr † has shown that section of the vagus prevents the secretion of gas into the air-bladder.

The evidence that it acts as a respiratory organ is very slight. Many fishes swallow air, but there is nothing to show that the air is taken into the air-bladder. In some cases however it has been shown (e.g. by Budgett, *op. cit.*, in young *Gymnarchus*) that the fish dies if it is prevented from coming to the surface to take in air. It has however been suggested with more probability that the oxygen secreted into the bladder may serve as a store when the fish enters water in which the supply of oxygen is too small.

In some fishes, e.g. the *Ostariophysi*, in which the posterior chamber is non-distensible and often enclosed by bone, while the anterior chamber is distensible and connected by ossicles to the membranous labyrinth, and in other fishes (see above) in which the air-bladder is in connection with the ear, it has been surmised, though not in any way proved, that the air-bladder acts as a resonator in intensifying sound vibrations and transmitting them to the auditory apparatus. On this view the Weberian apparatus may be of use in increasing the acuteness of hearing. It has also been suggested that it acts as a sound-producing organ, as a consequence of the incomplete septa and membranes which project into it being set in vibration by a movement of the contained air, caused by contraction of the extrinsic and intrinsic muscles which are contained in its walls. This suggestion rests on observation, for many fishes possess the power of producing sound (grunting, drumming, hissing, etc.), as many *Sciaenidae*, some *Siluridae* (*Doras*, *Platyostoma*, etc.), *Trigla gurnardus*, *Dactylopterus volitans*, *Malapterurus electricus*, and many others; and in some cases the sound has actually been detected

\* See Hübner, in *Arch. f. Anat. und Physiologie*, 1892, p. 54.

† C. Bohr, Influence of section of vagus on gas secretion in air-bladder, *Journ. of Physiology*, 15, 1894, p. 494-500.

proceeding from the air-bladder in fishes just removed from the water and opened. It appears that sounds may be produced in some fishes without special air-bladder muscles by the activity of muscles, with the fascia of which the air-bladder is in close connection (*Peristedion cataphractum*, *Trigla lyra*, *Sciaena aquila*, etc.).

**Vascular System.** The heart is without a conus arteriosus, and is usually separated from the ventral aorta by two semilunar valves only, though there is sometimes a small third valve. In some Clupeids it is said \* that a trace of a small conus provided with striped muscles may be made out, and in *Butirinus* (*Albula*) there are actually two rows of valves (two large and two small in the proximal, and two large in the distal row).

The ventral aorta presents at its ventricular end a swelling, the *bulbus arteriosus*, due to the thickness (elastic tissue and smooth muscular fibres) of its walls at this point. It gives off branches to the four anterior branchial arches, which usually bear gills.

The ventral aorta does not as a rule give off branches to arches which are without gills, but in some cases with deficient posterior gills (*Symbranchus*, *Amphipnous*, etc.) the afferent vessel from the ventral aorta is present and passes round directly into the efferent vessel, so that venous blood is conveyed into the dorsal aorta. As an example, we may mention *Amphipnous*, the first branchial of which has no gills; the second has a few filaments; the third has a transparent fringed membrane, and the fourth has no gills. The breathing organs are two sacs filled with atmospheric air and placed over the upper ends of the branchial arches; they open into the branchial cavity between the dorsal end of the hyoid and first branchial arches. The ventral aorta gives off a branch on each side, which passes to the fourth branchial arch and joins its fellow to form the dorsal aorta; it then gives off small branches to the second and third branchial arches and to the air-cavities, the blood from which is returned in two trunks which join the dorsal aorta.

The blood after passing through the gills is collected by the efferent branchial arteries, of which one leaves each gill-bearing arch. These fall into the two roots of the dorsal aorta, which anastomose in front dorsal to the parasphenoid bone and constitute the so-called *circulus cephalicus* (Fig. 120, *cc*). The *circulus cephalicus* gives off anteriorly the internal (at *a*) and external (*b*) carotid arteries, and receives an anastomosing branch from the hyoidean artery (*vh*); posteriorly it gives off the

\* J. E. V. Boas, *Morph. Jahrb.*, vi., 1880, p. 527.

two subclavian arteries, and on the right side the large coeliac artery (*r*). The hyoidean artery (*vh*) is a continuation of the ventral end of the efferent vessel of the first branchial arch on to

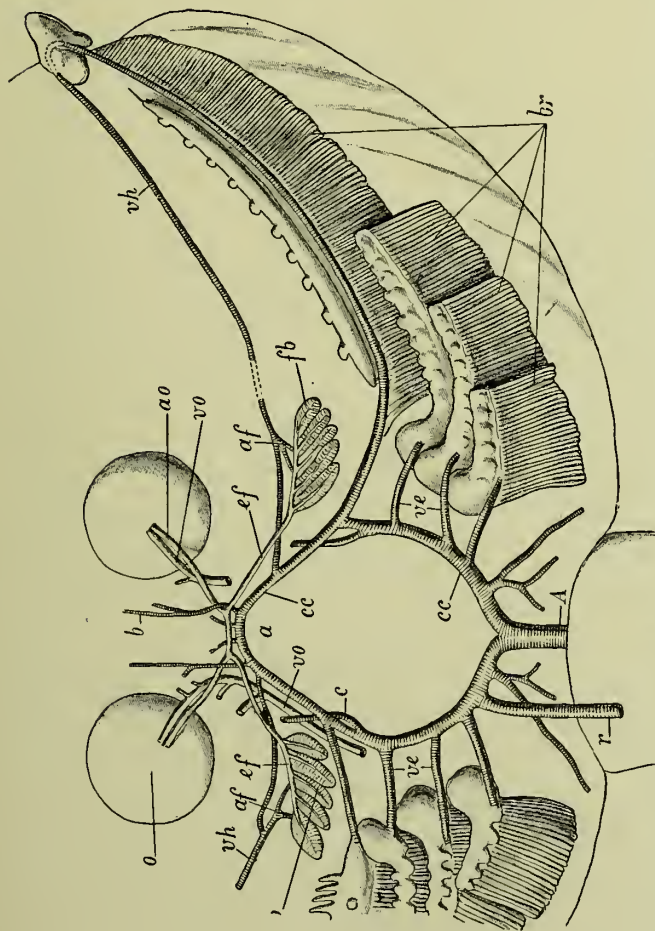


FIG. 120.—Dorsal arterial system of *Gadus callarias* (after J. Müller, from Perrier). A dorsal aorta; a anastomosis of the two roots of the dorsal aorta completing the cervical cephalic; at afferent vessels of the pseudobranch; ao ophthalmic artery; b external carotid; br branchiae; c posterior external carotid; ce trunks cephalic; e/ efferent vessels of the pseudobranch; f/ pseudo-branch; o eye; r coeliac artery; ze efferent branchial vessels; va vessel proceeding from the ventral end of the efferent vessel of the first-branchial arch to the pseudobranch; zo ophthalmic vein.

the hyoid, up which it runs in a dorsal direction to supply the pseudobranch (*fb*). The efferent vessel of the pseudobranch



(ef) anastomoses with its fellow of the opposite side and then passes round the external carotid to the choroid gland, a *rete mirabile* in the choroid coat round the entrance of the optic nerve into the eye. When the pseudobranch is not present, there is no choroid gland. In *Gymnarchus* the efferent vessels of the third and fourth branchial arches do not join the dorsal aorta but pass to the air-bladder.

The blood of the choroid gland supplies the choroid coat. The iris and sclerotic are supplied by the external carotid. The efferent branchial vessels give off small vessels for the nutrition of the branchial arch tissues, and near their ventral ends they give off vessels for the ventral part of the body, the neighbouring parts of the head, and even in some cases the heart. The hyoidean artery which supplies the pseudobranch is an example of this system of arteries.

The dorsal aorta is frequently closely adherent to the ventral wall of the vertebral column, so that the latter appears to form part of its wall. It may be swollen at intervals, and in some forms (*Esox*, *Clupea*, *Salmo*, *Silurus*, etc.) a fibrous elastic band projects into its cavity. The principal branches are subclavian, which may come off from the circulus cephalicus, the coeliaco-mesenteric which frequently gives off the air-bladder vessel and a posterior mesenteric.

The veins are arranged in the usual piscine fashion. The left posterior cardinal is often smaller than the right and appears as a small branch of the latter coming from the anterior part of the kidney; or the right vein may alone be present, lying almost in the middle line and receiving branchlets from each side. A renal-portal system appears to be present in most Teleosteans. The hepatic-portal vein may receive tributaries from the air-bladder, the gonads (*Perca*, *Blennius*, *Cyprinus*, *Osmerus*, etc.), and the ventral body wall (*Salmo*, *Alosa*, *Clupea*, etc.), though these veins more generally open into the posterior cardinals.

The **body-cavity** has the usual piscine arrangement. The pericardium is completely separated from the general body-cavity. Paired **abdominal pores** opening at the sides of the anus are absent in most Teleosteans, but they are found in the *Salmonidae* and *Mormyridae*, though not universally. They must not be confused with the pore-like oviducts of female *Salmonidae*, etc. (see below).

The urinary organs are paired streaks of kidney substance

\* M. Weber, *Morph. Jahrbuch*, 12, 1886, p. 336. Jungersen, *Arb. a. d. Zool. Inst. Würzburg*, 9, p. 93.



placed on the ventral side of the vertebral column between it and the air-bladder.

They have a great longitudinal extension, frequently reaching from the head to the end of the body-cavity, or even in some cases extending into the caudal region. Their front ends are enlarged into the so-called **head-kidneys**. The head-kidney, as was shown by Balfour, consists of lymphatic tissue which occupies the place of the pronephros of the larva. There are two longitudinal urinary ducts which unite posteriorly to form the single ureter. This structure, which frequently has a bladder-like dilatation, passes ventral-wards on one side of the air-bladder to open externally behind the anus, or into the rectum, into which the generative duct may also open (some *Symbranchii*, *Plectognathi*, *Pediculati*), or, in the *Pleuronectidae*, on a papilla placed asymmetrically on the coloured side of the body. Nephrostomata are never present.

The generative and urinary openings, whether separate or united, frequently open on a papilla which may be of some length (*Blenniidae*, *Gobiidae*, etc.). In *Rhodeus* the opening of the oviduct is prolonged in the breeding season into a tube, by means of which the female deposits her ova in the shells of living bivalves (Fig. 123). The ovaries are usually double, rarely single, saccular bodies the walls of which are continued into the short median oviduct which opens between the anus and the urinary opening, or with the latter. In some Telcosteans the ovaries are separate from their ducts, and the ova are dehiscent into the body-cavity whence they escape by two funnels which join to form a short tube which opens to the exterior usually between the anus and the ureter (*Salmonidae*, *Muraenidae*, etc.). In viviparous forms development takes place in the ovaries or in the oviduct. The testes are paired saccular bodies, and are apparently always

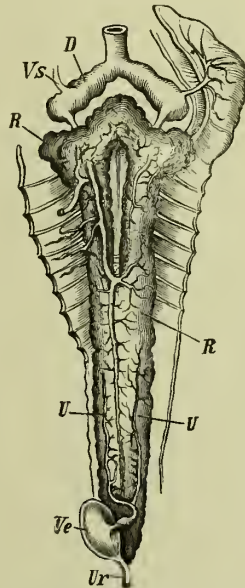


FIG. 121.—Kidneys of ♂ *Salmonfario* (after Hyrtl). *D* ductus Cuvieri; *R* kidneys; *U* ureter; *Ur* efferent duct of bladder; *Ve* bladder-like dilatation; *Vs* subclavian vein.

continuous with the short duct which either opens in the same position as in the female, or joins the ureter, so that there is a median *porus urogenitalis* behind the anus.

In the viviparous forms fertilisation is effected by an intromittent organ, which is usually formed by the urogenital papilla. A few Teleosteans (*Serranus*, etc.) are hermaphrodite.

The ova fall into the body-cavity and escape by porelike oviducts in the *Galaxiidae*, *Hyodontidae*, *Notopteridae*, *Muraenidae* and *Salmonidae*.

In *Fierasfer* there is said to be a pronephros in the adult, and the posterior part of the kidney is not developed.

The ova are always provided with soft shells and vary considerably in size; amongst the largest are those of *Gymnarchus* (10 mm.) and of *Arius* (5 to 18 mm.). They may be deposited singly (salmon, trout, etc.), or they may be agglutinated together by a substance secreted by the walls of the oviduct. In freshwater forms they either adhere to some foreign body or are deposited in nests; in marine forms they are either attached to foreign bodies or float freely in the surface waters of the ocean, or sink to the bottom as in the herring. Most fishes breed once a year at a definite period, but some breed more than once, and in some the breeding period is much prolonged—as in the cod and herring.

Care of the brood by the female is often found (*Aspredo*, *Solenostoma*, *Cichlidae*, see systematic part); in the male it is more frequent (by nests in *Gymnarchus*,\* *Heterotis*, *Cottus*, *Gastrosteus*, *Cyclopterus*, *Antennarius*, *Ophiocephalus*, *Callichthys*, etc.; in *Arius* the eggs are carried in the pharynx of the male, in Lophobranchs in a pouch on the abdomen).

The segmentation is meroblastic and the germinal layers arise by delamination. The cerebro-spinal cord is formed as a solid keel-like thickening of the ectoderm, which subsequently becomes hollow. The young are hatched at an early stage and undergo the remainder of their development as larvae. The larvae have a pronephros and considerable remains of the yolk-sac. The Teleostean pronephros is characteristic, in that the portion of the body-cavity containing the glomerulus is quite cut off from the rest and is in relation with the pronephric duct by one body-cavity opening only.

\* Budgett, Breeding Habits of some W. African Fishes, etc., *Trans. Zool. Soc.*, 16, 1901, p. 115.

Teleosteans frequently undergo remarkable changes of form in their growth. This is a marked feature of the group, and leads to some difficulty in the recognition of species. As examples may be mentioned the *Pleuronectidae*, *Cyttidae*, *Muraenidae*, *Xiphiidae*, *Plectognathi*. In many cases the young are so different that they have been described as distinct genera.

Moreover, Teleostean fishes are often highly variable under the influence of changed conditions (variation in acquired characters), particularly with regard to colour, both of skin and flesh. The change in the colour of the skin is due to the pigment cells (chromatophors).

Secondary sexual differences are usually present. The male is generally smaller than the female, and some of its fin-rays or fins may be prolonged. The male is often more brightly coloured in the breeding season, or its skin may become warty.

Hybridism is also known to occur (*Serranus*, *Pleuronectidae*, *Cyprinidae*, *Salmonidae*, etc.).

Some fishes are very long-lived (carp and pike to beyond 100 years), and growth frequently appears to be somewhat indefinite and to continue for a long time. Fishes which rapidly attain to their full size (e.g. sticklebacks) are said to be shortlived.

A few fishes have been domesticated and transported to different parts of the globe (carp, Crucian carp, tench, goramy), and certain species of salmon and trout have been acclimatised in countries in which they are not indigenous (see accounts of families).

Marine fishes are usually extremely sensitive to changes of temperature, freshwater fishes much less so. It is said that the carp will survive after being frozen in a block of ice. A modified hibernation has been observed in some Cyprinoids and Muraenoids in cold weather, and many tropical fishes (Siluroids, *Labyrinthici*, Ophiocephaloids, etc.) pass the dry season in a torpid state in hardened mud.

The flesh of many fishes is poisonous, and in unknown waters, especially in tropical seas, great care must be exercised in selecting fish for food.

The wounds caused by the spines of many fishes are poisonous. This is generally due to the poisonous nature of the mucus which covers the body, but it may be caused by special poison glands, as in *Synanceia*, *Thalassophryne*.

There is a considerable number of marine fishes which occasionally wander into freshwater and ascend rivers (e.g. *Sciaenidae*, *Pleuronectes*, species of *Clupeidae*), and a smaller number of freshwater fishes which occasionally descend into the sea (some species of *Salmo*, of Siluroids, of *Coregonus*, and pre-eminently the *Gastrosteidae* and *Cyprinodontidae*); but most of these are inhabitants of the brackish water. They must be distinguished from those fishes which migrate for the purpose of spawning. Such are of two kinds; there are the *anadromous* fishes which ascend rivers to spawn in freshwater, as the salmon and the salmon-trout, some Clupeids, etc., and *katadromous* fishes, like the freshwater eel, which descend to the sea to spawn. There are many clear cases of marine fish which by geological changes have been retained in freshwater basins; such are *Cottus quadricornis*, in the large lakes of Scandinavia; species of *Gobius*, *Blennius* and *Atherina* in the lakes of N. Italy; *Comephorus* in the depths of Lake Baikal.

The classification of the Teleostei adopted here is essentially that of Mr. G. A. Boulenger, F.R.S., to whom I am greatly indebted for having allowed me to see proofs of his work before its publication. It is as follows:\*

Sub-order 1. MALACOPTERYGII (SALMONICLUPEIFORMES).†

„ 2. OSTARIOPHYSI (CYPRINISILURIFORMES).

„ 3. SYMBRANCHII (SYMBRANCHIFORMES).

„ 4. APODES (ANGUILLIFORMES).

„ 5. HAPLOMI (ESOCIFORMES).

„ 6. HETEROMI (DERCETIFORMES).

„ 7. CATOSTEOMI (GASTROSTEIFORMES).

Tribe A. *Selenichthyes*.

„ B. *Hemibranchii*.

„ C. *Lophobranchii*.

„ D. *Hypostomides*.

„ 8. PERCESOCES (MUGILIFORMES).

„ 9. ANACANTHINI (GADIFORMES).

„ 10. ACANTHIPTERYGII.

Tribe A. *Perciformes*.

„ B. *Scombriformes*.

„ C. *Zeorhombi* (*Zeirhombiformes*).

„ D. *Kurtiformes*.

„ E. *Gobiiformes*.

„ F. *Discocephali* (*Echineiformes*).

„ G. *Scleroparii* (*Triglififormes*).

„ H. *Jugulares* (*Blenniiformes*).

\* Boulenger, *Ann. and Mag. Nat. Hist.* (7), 13, 1904, p. 161.

† The names in brackets are those used in the fish-gallery of the British Museum.

Tribe I. *Taeniosomi* (*Lophotiformes*).

## Sub-order 11. OPISTHOMI.

,, 12. PEDICULATI (LOPHIIFORMES).

,, 13. PLECTOGNATHI (BALISTIFORMES).

Tribe A. *Sclerodermi*.,, B. *Gymnodontes*.

The old group *Physostomi* (with a ductus pneumaticus to the air-bladder), which is sometimes referred to in the preceding pages, included, roughly speaking, the *Malacopterygii*, *Ostariophysi*, *Symbranchii*, *Apodes*, *Haplomi*, *Heteromi* (in part), and *Perceoces* (in part), of the above classification.

## Sub-order 1. MALACOPTERYGII (SALMONI-CLUPEIFORMES).

Soft-rayed fishes with the anterior vertebrae simple, unmodified, and without auditory ossicles; symplectic present or absent; opercular bones distinct; pharyngeal bones simple above and below, the lower not falciform. Pectoral arch suspended from the skull; mesocoracoid always well developed. Maxillary bone forming part of margin of upper jaw; no barbels. Supra-occipital sometimes separated from the frontals by the parietals. Gills 4, a slit behind the fourth. Air-bladder if present with a pneumatic duct. Dorsal and anal fins without true spines. Pelvic fins abdominal, sometimes absent; scales usually cycloid, sometimes ctenoid; occasionally absent. No developed photophores. Adipose fin present or absent. This sub-order of Teleostei is nearest to the Ganoids.

Fam. 1. **Leptolepidae**. Extinct. Upper Lias to Lower Cretaceous; vertebral centra nearly complete, pierced by the notochord; without fulcra; scales cycloid. *Leptolepis* Ag., *Thrissops* Ag.

The **Pholidophoridae** (p. 180), **Oligopleuridae** (p. 182), and the **Archaeomaenidae**, all extinct, are placed here by Smith Woodward and Boulenger.

Fam. 2. **Mormyridae**.\* Body and tail scaly; head scaleless; upper jaw formed by the two premaxillaries which are fused, and by the maxillaries. Sub- and very small inter-operculum present; supraoccipital separated from frontals by parietals. On each side of the skull there is a large cavity leading into the interior and covered by a thin bony lamella. They are without pharyngeal teeth. All the fins are well developed in *Mormyrus*, caudal, anal and pelvic fins are absent in *Gymnarchus*. No adipose fin. Pectorals directed upwards. Pseudobranch absent, gill-apertures reduced to a short slit. Air-bladder simple, communicating with the ear. Two pyloric caeca. A series of pores along

\* Kölliker, *Bericht v. d. zootom. Anstalt zu Würzburg*, 1849. Hyrtl, *Denkschr. Akad. Wiss. Wien*, 1856, xii. p. 1. Erdl., *Münchner Gelehrte Anzeigen*. Boulenger, *Poissons du Bassin du Congo*, 1901.



the base of the dorsal and anal (if present) fins. f. w. of tropical Afr. They possess an electric organ on each side of the tail with feeble electric functions, consisting of modified muscle-tissue. The snout frequently of strange shape; eyes often reduced. The brain is remarkable for its size; 10 genera. *Mormyrus* L., teeth in rows along the middle of the palate and the tongue; *M. oxyrhynchus* Geoff., venerated by the ancient Egyptians; *Hyperopisus*, *Mormyrops*; *Gymnarchus* Cuv., Nile and W. Afr. rivers, eel-like, each jaw with incisor-like teeth; air-bladder cellular, very extensible, duct with sphincter at oesophageal opening; lays very large eggs; the gills of the embryo project beyond the gill-openings. *Gnathonemus*.

Fam. 3. **Clupeidae**. Body covered with scales, head naked; supra-occipital in contact with frontal. Abdomen frequently compressed into a serrated edge. Maxillaries (of three pieces) and premaxillaries both enter into upper jaw. Opercular apparatus complete. Adipose fin absent, dorsal not elongate, anal sometimes very long. Stomach with blind sac, pyloric caeca numerous. Gill openings usually wide. Pseudobranch usually present. Air-bladder simple, large, communicating with the ear. Principally coast fishes; none from the deep sea; may enter f. ws. communicating with sea; temp. and trop. zones. Many fossil forms. *Engraulis* C. et V., anchovies, upper jaw prominent; mouth with a very deep cleft; eyes covered by skin; *E. encrasicolus* L. (*Anchovia* J. and E.), the anchovy, abundant in Med., also taken in E. Channel; *Cetengraulis* Gthr.; *Stolephorus* Lac.; *Coilia* Gray; *Dussumieria*; *Etrumeus*; *Chatoessus* C. et V. (*Dorosoma* Raf.), C. Amer., Aust., E. Ind., Japan. *Clupea* Cuv., herrings, upper jaw not projecting, eyes with free lateral adipose lids, more than 60 species, most used as food, but some trop. species poisonous; *C. harengus* L., the herring, incredibly prolific, whitebait consists chiefly of the young of the herring (and sprat), the air-bladder opens into the stomach, and also on the left side near the anus,\* the eggs are attached to stones, etc.; *C. pilchardus* Walb. (*Clupanodon* Lac.), the pilchard (the young is the sardine), equally abundant in Brit. Channel, on coast off Portugal and in Med.; *C. sprattus* L., the sprat, in Norfolk sold as anchovies; *C. alosa* L. (*Alausa*, *Alosa*), the shad or allice-shad, coasts of Eur. ascending rivers; *C. finta*, the twaite-shad. Other Clupeoid genera are *Clupeoides*, *Pellonula*, *Clupeichthys*, *Pellona*, (*Ilisha*), *Pristigaster*, *Chirocentrodon*, *Pomolobus*, *Sardinella*, *Opisthonema*, *Brevoortia*, *Opisthopecterus*, *Odontognathus*, *Pristigaster*; *Chanos* Lacép. with accessory branchial organ† in a cavity behind the gill-cavity, Indo-Pac., 4 ft., edible.

The following genera may be placed here: *Elops*, *Megalops* (*M. atlanticus*, the tarpon), *Albula* (*Butirinus*) with a trace of the *conus* (with two rows of valves) in the heart; *Pterothrissus* (*Bathyrhissa*), deep sea, Japan.

Fam. 3a. **Hyodontidae** (moon eyes), f. w. fish of N. America, no oviducts; *Hiodon*, Le Su.

Fam. 4. **Alepocephalidae**. Deep-sea fishes approaching the Salmonoids; without adipose fin or air-bladder. Phosphorescent spots none or small. Stomach curved, without blind sac; pyloric caeca in moderate number. Pseudobranch present. *Alepocephalus*, *Mitchillina*, *Bathytroctes*, *Talismania*, *Conocara*, *Platytröctes*, *Aleposomus*.

\* Weber, "De aure et auditu," 1, 1820, vii., 63.

† J. Müller, *Bau u. Grenzen d. Ganoiden*, p. 75.

Fam. 5. **Notopteridae**, with one genus *Notopterus*, f. w. of E. Ind. and W. Afr.

Fam. 6. **Osteoglossidae**. Body covered with large mosaic-like scales ; head scaleless, its integument confluent with the bone ; dorsal fin on tail and opposite anal ; gill openings wide, pseudobranch absent ; air-bladder simple or cellular, stomach without caecal sac, pyloric appendages two. Eggs fall into body cavity. Large f. w. fishes of the tropics. 4 genera. *Osteoglossum* Vandelli, S. Amer. ; *Arapaima* Müll., Brazil and Guyanas ; *Heterotis* Ehr., trop. Afr. ; *Scleropages*, Australia, E. Ind. Arch. Excluding the E. Ind. Archipelago, the distribution of this family is the same as that of the Dipnoi. *Heterotis niloticus* forms a nest and the young larvae have external gills.

Fam. 7. **Pantodontidae**. One genus, f. w., W. Afr., pectorals very large.

Fam. 8. **Ctenothrissidae**. Extinct, Cretaceous.

Fam. 9. **Phractolaemidae**. One genus, W. Afr.

Fam. 10. **Saurodontidae** (*Ichthyodectidae*). Extinct, Cretaceous ; *Portheus*, *Ichthyodectes*.

Fam. 11. **Chirocentridae**. One genus, Ind. Ocean and Seas of China and Japan.

Fam. 12. **Salmonidae**. Body generally covered with scales, head scaleless ; margin of upper jaw formed by maxillaries and premaxillaries ; a small adipose fin behind the dorsal ; pyloric caeca generally present and numerous ; air-bladder large and simple with a pneumatic duct ; pseudobranch present ; no oviducts. Inhabitants of sea and f. w. ; most of the mar. genera are from the deep sea ; most of the f. w. forms are peculiar to the temperate and arctic region of the Northern Hemisphere, one occurring in New Zealand ; many f. w. species are anadromous ; no fossils of f. w. species known. *Osmerus* and other genera from the Miocene.

*Salmo* Art., trout, salmon and charr, inhabitants of f. w., many species descending to the sea after spawning (anadromous), the young of all are barred, the bars vanishing in adult except in small varieties ; many of the species are highly variable and capable of considerable adaptation to their surroundings ; the marine forms usually silvery with or without black spots, the f. w. forms more or less speckled with black and red. Some individuals of full size are sterile, but this is probably only a temporary condition ; overgrown individuals are sterile ; anadromous fish, generally return to their native river. River and sea trout have been acclimatised in Tasmania and N. Zealand, and apparently in India. As these species are highly variable in response to change of condition the observation of these acclimatised races will afford an extremely interesting study.

*S. salar* L., salmon, N. Hemisphere between latitudes 45° and 75° ; does not occur in rivers opening into Med.\* the last Thames salmon was caught in 1833 ; a marine fish ascending rivers to spawn (Sep. to Jan. in Britain), the nest or redd is dug out by the female in gravel and the eggs are buried ; young salmon of the first and second year are called *parr* or *pink* (4 to 6 in.) ; they then become *smolts*, which descend to sea, and reascend the rivers as *grilse*, which having spawned go to the sea and return as salmon ; a salmon which has spawned is a *kelt*, kelts go to the sea, and probably reascend next year ; *kipper* is a male kelt, or a salmon which has been detained in f. w. and got

\* Not even in those of Macedonia, notwithstanding Fluellen (Henry V., Act 4, Sc. 7) !

lean; male parrs may become sexually mature and fertilise the eggs of a full-grown female; will hybridise (artificially) with the trout and charr; not a highly variable species and change of conditions is fatal. The various kinds of British trout are probably all varieties of the same species, as they will freely cross, but three species may for convenience be distinguished: *S. trutta* Flem., sea- or salmon-trout, phinok, sewin, a migratory species; *S. fario* L., the brook trout; and *S. levenensis* Walker, Loch Leven trout. To these the bull-trout, *S. eriox*, and great lake-trout, *S. ferox*, may possibly be added.

*S. alpinus* L., the charr, breed Nov. to Dec.; redd usually in gravelly shallows in the lakes (the Windermere charr is known as *S. willughbii*); the charrs are migratory or non-migratory and inhabit the deep waters of lakes; there appears to be one British species with several varieties. *S. fontinalis* Mitchell, f. w. of Brit. N. Amer., acclimatised in Britain. *Oncorhynchus* Suckley, anadromous fish in American and Asiatic rivers flowing into the Pacific; *O. tshawytscha*, the Californian salmon; *Brachymystax* Gthr., Siberian rivers; *Lucio-trutta* Gthr. (*Stenodus* Rich.), Arctic N. Amer.; *Plecoglossus* Schley., f. w. of Jap. and Formosa. *Osmerus* L., smelts, migratory, ascending rivers to spawn and frequently becoming resident in them, Atl. coasts of N. Eur. and N. Amer.; *O. eperlanus* L., the smelt, spangling, irregular in its migrations, spawning in rivers near high-water mark, generally found in rivers from Aug. to May, spawns about March or April, when fresh exceedingly good eating, but deteriorate in a few hours; allied genera are *Hypomesus* and *Thaleichthys* from the Pacific coast of N. Amer., the latter, known as Oulachan, has so much oil it will burn like a candle; *Mallotus* Cuv.; *Coregonus* Art. (*Argyrosomus* Ag.), whitefish, mostly lacustrine, a few anadromous, northern parts of temp. Eur., Asia, and N. Amer.; *C. oxyrhynchus* L., houting, marine entering f. w. Holland, Germany, Denmark; *C. chupeoides* Lac., schelly, f. w. of Lake District and Wales; *C. vande-sius* Rich., vendace, f. w. lochs of Scotland; *C. pollan*, Thomps., pollan, f. w. of Ireland; *Thymallus* Cuv., graylings, clear streams of Eur., Asia, and N. Amer.; *Th. vulgaris* Nilss., grayling, flesh good, in best condition Oct. and Nov.; *Salanx* Cuv.; deep-sea genera are *Argentina*, *Microstoma*, *Bathylagus*.

Fam. 13. **Stomiidae**. Scales absent or thin; a hyoid barbel; eyes large; luminous spots more or less developed; no pseudobranch; oviducts present. Deep-sea fishes descending to the greatest depths and distinguished by their barbel and formidable dentition. *Astronesthes* Rich., *Stomias* Cuv., *Echiostoma* Lowe, *Grammatostomias* G. and B., *Photoneustes* Gthr., *Malacosteus* Ayres, *Bathypheis*, *Chauliodus* Bloch and Schneider, *Bathylaco*, *Maurolicus*, *Sternoptyx*, etc.

Fam. 14. **Gonorhynchidae**, one genus, Aust. and Japanese seas.

Fam. 15. **Cromeriidae**, with one genus *Cromeria*, recently discovered in the White Nile.

## Sub-order 2. OSTARIOPHYSI (CYPRINI-SILURIFORMES).

The anterior vertebrae are co-ossified and have some of their lateral elements detached to form a chain of small bones, the Weberian ossicles, which connect the air-bladder with the ear (p. 202). The air-bladder is probably always present though

it may be very small. When well developed it has a pneumatic duct. Pectoral arch suspended from the skull, mesocoracoid present. The great majority of freshwater fishes are included in this sub-order.

Fam. 16. **Characinidae**. Body scaly, head naked; barbels absent, margin of upper jaw usually formed by the premaxillaries and maxillaries, rarely by the premaxillaries only; jaws usually toothed; parietals distinct from supraoccipital; symplectic present; generally a small adipose fin behind the dorsal; pelvics abdominal; pyloric appendages more or less numerous; air-bladder divided into two portions; pseudo-branch absent or much reduced. Freshwaters of Africa and of tropical America. In America they replace the Cyprinoids; unknown as fossils.

**Erythrinina**. Adipose fin absent; trop. Amer. The genera are *Macrodon*, *Erythrinus*, *Lebiasina*, *Nannostomus*, *Pyrhulina*, *Corynopoma*.

**Curimatina**. A short dorsal and an adipose fin; dentition imperfect; trop. Amer.; *Prochilodus*, *Caenotropus*, *Hemiodus*, *Saccodon*, *Parodon*.

**Citharinina**. A rather long dorsal and an adipose fin; minute labial teeth; trop. Afr. *Citharinus* Cuv., attaining to 3 ft.

**Anastomatina**. Short dorsal and an adipose fin; teeth in both jaws well developed; the gill membranes grown to the isthmus; nasal openings remote from each other; trop. Amer. *Leporinus*, *Anastomus*, *Rhytiodus*.

**Nannocharacina**. Like the last, except that incisors are notched, and nostrils close together. *Nannocharax*.

**Tetragonopterina**. Short dorsal and an adipose fin; teeth well developed, notched or denticulated; gill-membranes free from the isthmus; nasal openings close together; S. Amer. and trop. Afr. *Alestes* M. and T., trop. Afr.; *Tetragonopterus* Cuv., trop. Amer. Of the other genera *Nannaethiops* and *Bryconae-thiops* are African, the rest are S. American, viz., *Chirodon*, *Megalobrycon*, *Gastrolepecus*, *Piabucina*, *Scissor*, *Pseudochalceus*, *Aphyocharax*, *Chalceus*, *Brycon*, *Chalcinopsis*, *Bryconops*, *Creagrutus*, *Chalcinus*, *Piabuca*, *Paragoniates*, *Agoniates*.

**Hydrocyonina**. Short dorsal and adipose fin; teeth well developed and conical; gill-membranes free from the isthmus; nasal openings close together. S. Amer. and trop. Afr. Fishes of prey. *Hydrocyon* Cuv., trop. Afr., and *Cynodon* Spix., S. Amer., both to 4 ft. Except *Sarcodaces* from W. Afr. the other genera are trop. Amer., e.g., *Anacyrtus*, *Hystricodon*, *Salminus*, *Oligosarcus*, *Xiphorhamphus*, *Xiphostoma*, etc.

**Distichodontina**. Dorsal fin rather elongate, adipose fin present; gill-membranes attached to the isthmus; belly rounded. Trop. Afr. *Distichodus* M. and T.

**Ichthyborina**. An adipose fin; dorsal rays 12 to 17; gill-membranes free from the isthmus; belly rounded; canine teeth; trop. Afr. *Ichthyborus* Günth., Nile; *Eugnathichthys*, *Phago*, W. Afr.

**Crenuchina**. Dorsal fin rather elongate, an adipose fin; gill-membranes free from the isthmus; belly rounded; without canine teeth. *Crenuchus* Günth., Brit. Guiana; *Xenocharax*, W. Afr.



**Serrasalmonina.** The caribe. Dorsal fin rather elongate; an adipose fin; gill-membranes free from the isthmus; belly serrated; trop. Amer.; exceedingly voracious, they assail persons entering the water. *Mylesinus*, *Serrasalmo*, *Myletes*, *Catoprión*.

Fam. 17. **Gymnotidae** (γυμνός naked, νῆτος back). Head scaleless; barbels none; body eel-shaped; scales small or absent; margin of upper jaw formed by premaxillaries and by maxillaries; anterior vertebrae united, modified, with Weberian ossicles; dorsal fin absent or reduced to adipose strip, caudal generally absent; tail ending in point, can be regenerated; anal long, pelvics absent; anus on or near the throat; shoulder girdle attached to skull; ribs well developed; gill-openings narrow; air-bladder double; stomach with caecal sac; pyloric caeca present; ovaries with oviducts. Eel-like f. w. fishes from S. America. *Sternarchus* Cuv., *Rhamphichthys* M. and T., *Sternopygus* M. and T., *Carapus* M. and T., *Gymnotus* Cuv. (*Electrophorus*), electric eel, Brazil and Guyanas, electric organ along each side of the tail; *Giton* Kaup, *Eigenmannia* J. and E.

Fam. 18. **Cyprinidae**. Body generally covered with scales; head naked. Anterior 4 vertebrae modified and joined, margin of the upper jaw formed by the premaxillaries. Belly rounded or if trenchant without ossifications. No adipose fin; a dorsal and anal fin, pelvic fins abdominal. Stomach without blind sac. Pyloric appendages absent. Mouth toothless; lower pharyngeal bones well developed, falciform, sub-parallel to the branchial arches, provided with teeth in one, two, or three series. Air-bladder large, divided into an anterior and posterior portion by a constriction, or into a right and left portion, enclosed in an osseous capsule. Ovarian sacs closed. About 200 genera and 1,200 species; freshwaters of the Old World and N. America. The fossil forms can be referred mostly to living genera.

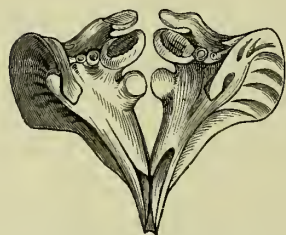


FIG. 122.—Lower pharyngeal bones of a carp (after Heckel and Kner, from Claus).

I. **Catastomina.** Pharyngeal teeth in a single series, numerous; dorsal fin long, anal short; barbels none. Lakes and rivers of N. Amer., 2 spec. from N.-E. Asia, generally known as suckers. *Ictiobius* Raf., *Carpiodes* Raf., *Cycleptus* Raf., *Pantosteus* Cope, *Catostomus* Le Sueur, *Chamistes* Jordan, *Xyrauchen* Eig. and Kirsch, *Erismyzon* Jordan, *Minytrema* Jordan, *Moxostoma* Raf., *Placopharynx* Cope, *Lagochila* Jord. and Bray.

II. **Cyprinina.** Anal fin short with not more than 5 or 6, rarely 7, branched rays. Abdomen not much compressed. Barbels often present, never more than 4. Three branchiostegals. Air-bladder without osseous covering.

*Cyprinus* Art., carps; large scales; dorsal fin long with its last undivided ray osseous and serrated; pharyngeal teeth in three rows, molar-like (Fig. 122); four barbels. *C. carpio* the carp, indigenous in Persia and China, introduced into Europe (known 1258 A.D.), into England (known 1496); food vegetable and animal; bury themselves in mud in winter, will live for some time out of water, may attain a large



size (20–50 lb.), and great age (50–100 years, Gesner, Buffon), very prolific, spawn on weeds about May, said to form hybrids with the Crucian carp with the tench and the bream. *Carassius* Nilsson, without barbels; *C. vulgaris* Nilss., the Crucian carp, Prussian carp, Eur. and Siberia; *C. auratus* L., gold-fish, China and Japan, introduced into Eur. and Amer. as an aquarium fish and naturalised in many streams; very variable under domestication in colour and otherwise, brilliancy generally decreases when turned into the open, in the wild state greenish; so-called telescope-fish is a variety; breeds in May and June. *Catla* C. and V., E. Ind.; *Labeo* Cuv., Afr. and E. Ind.; *Discognathus* Heck., Ind., Ceylon, S.-W. Asia, Afr.; *Capoëta* C. and V., W. Asia; *Barbus* Cuv., barbels, 200 species, Eur., Asia, Afr., dorsal fin with the (third) longest simple ray sometimes enlarged and serrated only exceptionally with more than nine branched rays commencing opposite or nearly opposite the root of the pelvic fin; eyes without adipose eyelid; mouth arched without inner folds; lips without horny covering, barbels 4, 2 or 0; *B. vulgaris* Fleming, Europe, to 50 lb., as food coarse, roe sometimes poisonous. *Thynnichthys* Bleek, E. Ind.; *Oreinus* McClell., Himalayas; from same region *Ptychobarbus*, *Gymnocypris*, *Schizopygopsis*, *Diptychus*; *Gobio* Cuv., Eur. a small maxillary barbel; dorsal fin with few rays, without spine; *G. fluviatilis* Flem., the gudgeon. Allied are *Ladislavia* and *Pseudogobio*, E. Asia; *Ceratichthys* Baird and Gerard, N. Amer., called chub in the U. S.; similar genera of N. Amer., and generally called “minnows,” are *Pimephales* (black head), *Hyborhynchus*, *Hybognathus*, *Camptostoma* (stone-lugger), *Ericymba*, *Cochlognathus*, *Exoglossum* (stone-toter or cut-lips), *Rhinichthys* (long-nosed dace). Other Old World genera are *Cirrhitina*, *Dangila*, *Osteochilus*, *Barynotus*, *Tylognathus*, *Abrostomus*, *Crossochilus*, *Epalzeorhynchus*, *Barbichthys*, *Amblyrhynchichthys*, *Albulichthys*, *Aulopyge*, *Bungia*, *Pseudorasbora*.

III. **Rohteichthyina.** Anal fin very short, with not more than six branched rays; dorsal fin behind pelvic; abdomen compressed; no barbels; pharyngeal teeth in triple series. *Rohteichthys* Bleek, East Ind. Arch.

IV. **Leptobarbina.** Anal fin as in last; dorsal opposite pelvic; abd. not compressed; barbels present, not more than 4; pharyngeal teeth in triple series. *Leptobarbus* Bleek, E. Ind. Arch.

V. **Rasborina** with *Rasbora*, from E. Ind. Cont. and Arch. and E. Afr.; *Amblypharyngodon*, *Luciosoma*, *Nuria* and *Aphyocypris*, from E. Ind. Cont.

VI. **Semiplotina** with *Cyprinion* from Syria, Persia, *Semiplotus* from Assam.

VII. **Xenocypridina** with *Xenocypris* and *Paracanthobrama* from China, *Mystacoleucus* from Sumatra.

VIII. **Leuciscina.** Anal fin of short or moderate length, with 8–11 branched rays, not extending forwards below the dorsal, which is short and without osseous ray. Barbels generally 0; pharyngeal teeth in a single or double series. *Leuciscus* Klein, white-fish, north temperate zone of both hemispheres; species found in England are *L. rutilus* Flem., the roach, said to form hybrids with the bream and rudd; *L. cephalus* Flem., the chub; *L. vul-*

*garis* Flem., the dace; *L. erythrophthalmus* Flem., the rudd or red-eye; *L. phoxinus* Flem., the minnow; *L. idus*, the id or nerfling, found in Europe, is domesticated in Germany, assuming the golden hue of semialbinism like a goldfish. *Tinca* Cuv., Eur. and Asia Minor, has been acclimatised in India, *T. vulgaris* Cuv., the tench, golden tench as a variety, due to albinism, as in the id and goldfish. *Leucosomus* Heck., N. Amer., *L. pulchellus* (fall-fish, dace or roach), *L. corporalis* (chub), *Chondrostoma* Ag., Eur. and W. Asia; other Old World genera are *Myloleucus*, *Ctenopharyngodon*, *Paraphoxinus*; N. American are *Mylopharodon*, *Meda*, *Orthodon*, *Acrochilus*.

IX. **Rhodenina** with genera *Achilognathus*, *Acanthorhodeus*, *Rhodeus*, *Pseudoperilampus*, roach-like fishes in East. Asia and Japan; in the females a long external urogenital tube is developed externally in the breeding season; this deposits the large eggs into the mantle cavity of the pond mussel where they develop. *Rh. amarus*, the bitterling (Fig. 123), extends into Europe.

X. **Daninina**. Small fish from E. Ind. Cont., Ceylon, E. Asiatic Islands, and a few from Afr. rivers; *Danio*, *Pteropsarion*, *Aspidoparia*, *Barilius*, *Bola*, *Scharca*, *Opsariichthys*, *Squaliobarbus*, *Ochetobius*.

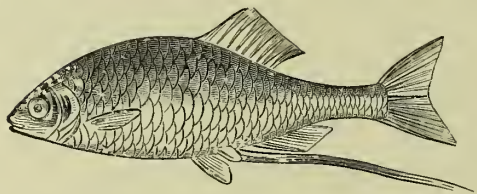


FIG. 123.—*Rhodeus amarus*, female (after v. Siebold, from Claus).

#### XI. Hypophthalmichthyina.

With *Hypophthalmichthys* from China.

#### XII. Abramidina.

Anal fin elongate; abdomen or part of the abdomen compressed. *Abramis* Cuv., the breams, temperate

parts of both northern hemispheres; *A. abramis* Flem., *A. blicca* Ag., both in Britain and Europe, hybrids between these two species and even other cyprinoids are not rare (Günther); *A. ballerus* L., the zope, *A. vimba* L., the zarthe, Europe; *A. crysoleucas* Mitchell, shiner, bream, United States. *Aspius* Ag., E. Eur. to China; *Alburnus* Heckel, bleak, Eur., W. Asia; *A. lucidus* Heck. u. Kner, Britain, Eur. north of Alps, absent in Scotland and Ireland; other genera are *Leucaspis* and *Pelecus*, Europe; *Pelotrophus*, E. Afri.; and the rest, *Rasborichthys*, *Elopichthys*, *Acanthobrama*, *Osteobrama*, *Chanodichthys*, *Hemiculter*, *Smiliogaster*, *Toxabramis*, *Culter*, *Eustira*, *Chela*, *Pseudolabuca*, *Cachius*, from E. Ind. or temp. Asia.

XIII. **Homalopterina**. Air-bladder absent, hill streams in E. Ind., genera *Homaloptera*, *Gastromyzon*, *Crossostoma*, *Psilorhynchus*.

XIV. **Cobitidina**. Loaches. Barbels 6 or more; dorsal fin short or of moderate length, anal fin short; scales small or absent; pharyngeal teeth in single series; air-bladder partly or entirely enclosed in bony capsule; pseudobranch absent. *Misgurnus* Lacép., Eur. and Asia, *M. (Cobitis) fossilis* Lacép., largest European loach; *Nemacheilus* v. Hass., Eur., Asia, Abyssinia, without spine

near orbit; *N. barbatula* Günth., groundling, stone-loach, etc., Britain and Europe; *Cobitis* Artedi, Eur., E. Ind.; *C. taenia* L., spined loach, with preorbital spine, Britain (rare) and Europe; *Botia* Gray, E. Ind.; from tropical India are *Lepidoccephalichthys*, *Acanthopsis*, *Oreonectes*, *Paramisgurnus*, *Lepidocephalus*, *Acanthophthalmus*, *Apua*.

Fam. 19. **Siluridae**. Cat-fishes. Skin naked or with osseous scutes, without scales. The 4 anterior vertebrae joined. Barbels always present; maxillary bone small, almost always forming a support to a maxillary barbel. Margin of the upper jaw formed by the premaxillaries and maxillaries or by the premaxillaries only. Parietal bones confluent with the supra-occipital. Sub-operculum absent. Adipose fin present or absent. Pyloric appendages absent. Mostly inhabitants of the fresh waters of all the temperate and tropical regions, some entering the salt water, but keeping near the coast; some are said to be able to cross land in search of other waters (*Callichthys*, *Clarias*, etc.). Over 100 genera and upwards of 1,000 species known. *Clarias* Gronov., Africa and S. Asia, muddy and marshy waters, an accessory branchial organ is attached to the convex side of the second and fourth branchial arches; Nilotic species known as Carmoot. *Heterobranchus* G. St. Hil., Afr. and E. Ind. Arch., acc. gills as in *Clarias*; *Plotosus* Lacép., brackish waters of Indian Ocean and Aust., brackish waters of Aust.; *Copidoglanis* Günth., *Cnidoglanis* Günth., *Chaca* C. and V., East Indies; *Saccobranchus* C. and V., E. Ind., gill-cavity with accessory posterior sac with contractile walls, vessels from last branchial artery and delivering into aorta. *Silurus* Art., temperate palaearctic rivers, *S. glanis* L., the wels, Europ. rivers east of the Rhine, to 300-400 lb. African genera are *Schilbe*, *Eutropius*; E. Indian are *Silurichthys*, *Wallago*, *Belodontichthys*, *Eutropichthys*, *Cryptopterus*, *Callichrous*, *Hemisilurus*, *Siluranodon*, *Ailia* *Schilbichthys*, *Lais*, *Pseudeutropius*, *Pangasius*, *Helicophagus*, *Silondia*. *Hypophthalmus* C. and V., S. Amer., eye behind and below angle of mouth, *Helogenes* Günth., *Bagrus* C. and V., Nile, *B. bayad*; African genera are *Chrysichthys*, *Clarotes*; E. Indian are *Macrones*, *Pseudobagrus*, *Liocassis*, *Bagroides*, *Bagrichthys*, *Rita*, *Acrochordonichthys*, *Akysis*. *Amiurus* (*Ameiurus*) Raf., horned pout, cat-fishes of N. Amer., one sp. in China; from N. Amer. also are *Hopladelus*, *Noturus*. *Platystoma* Ag., S. Amer. snout long, spatulate; allied are *Sorubim*, *Hemisorubim*, *Platystomichthys*, *Phractocephalus*, *Piramutana*, *Platynemichthys*, *Piratinga*, *Bagropsis*, *Sciades*, all from S. Amer. *Pimelodus* Lacép., 40 S. Amer. sp., 2 W. Afr. sp.; allied are *Pirinampus*, *Conorhynchus*, *Notoglanis*, *Callophysus*, *Lophiosilurus*, all from S. Amer. *Auchenoglanis*, trop. Afr.; *Arius* C. and V., 70 sp., in all trop. countries and seas; allied are *Galeichthys*, S. Afr. and Amer., mar.; *Genidens*, *Paradiplomystax* Brazil; *Diplomystax* Chili; *Aelurichthys* C. and S. Amer.; *Hemipimelodus*, *Ketengus*, *Osteogeniosus*, *Batrachocephalus* E. Ind.; *Atopochilus* W. Afr.

*Bagarius* Bleek, E. Ind.; *Euglyptosternum* Bleek, Syria; *Glyptosternum*, Hara, *Ambliceps* E. Ind.

*Doras* C. and V., *Oxydoras* Kner, *Rhinodoras* Kner, these three genera travel over land in the dry season in search of a pond of greater capacity, they make nests and both sexes tend the eggs, tropical S. Amer. in rivers flowing into the Atlantic; the following also are S. American, *Ageniosus*, *Tetranemichthys*, *Euanemus*, *Auchenipterus*,

*Glanidium*, *Centromochlus*, *Trachelyopterus*, *Cetopsis*, *Astrophysus*; *Synodontis* C. and V., trop. Afr.

*Callomystax* Günth., Bengal, *Mochocus* Joannis. *Rhinoglanis* Günth., Upper Nile.

*Malapterurus* Lac., electric cat-fish, trop. Afr., electric organ extends over whole body beneath the skin.\*

*Stygogenes*, *Arges*, *Brontes* and *Astroplebus* in the lakes and torrents of the Andes, Humboldt thought they lived in subterranean waters and were ejected by volcanoes; *Callichthys*, similar in dist. and habits to *Doras* (p. 221); *Chaetostomus* with the allied *Plecostomus*, *Liposarcus*, *Pterygoplichthys*; *Rhinelepis*, *Acanthicus*, *Xenomystus*, from f. w. of S. Amer.; *Hypoptopoma*; *Loricaria* L., trop. Amer., *Acestra* Kn., Brazil, Surinam; *Sisor*, N. India; *Erethistes* M. and T., Assam; *Pseudecheneis* Blyth, Himalayas; *Exostoma* Blyth, E. Ind. continent.

*Aspredo* L., Guiana, the female attaches the eggs to the spongy integument of its belly by pressing against them; *Bunocephalus*, *Bunocephalichthys* and *Harttia* from trop. Amer.

*Heptapterus*, *Nematogenys*, *Trichomycterus*, *Eremophilus*, *Pariodon* are small S. American forms from f. w. of high altitudes to 14,000 ft.; they resemble the loaches of the N. Hemisphere in appearance and habits.

*Stegophilus* Rein., and *Vandellia* C. and B., small fishes from Brazil, the latter are said to ascend urethra of persons bathing, but there is no doubt that they enter the gill-cavity of larger fishes.

*Cathorops* Jordan and Gilbert, Panama; *Ictalurus* Raf., f. w. of N. Amer.

### Sub-order 3. SYMBRANCHII.

Body eel-shaped. Shoulder-girdle usually joined to the skull; no mesocoracoid. Scales minute or absent. No paired fins. Unpaired fins reduced. Anus far from head. No air-bladder; gill-openings confluent in a single slit. Stomach without caecum and pyloric caeca. Ovaries with oviducts. Widely distributed in warm seas and freshwaters.

Fam. 20. **Symbranchidae**. Eel-like, without paired fins, scales minute or absent; gill-openings confluent into one slit on the ventral surface; anus far from head; no air-bladder, stomach caecum or pyloric caeca; with oviducts; f. w. and brackish w. of trop. Amer.; 3 genera, and one marine genus (*Chilobranchus*) from Australia. *Amphipnous* Müll., Bengal, 3 branchial arches of which the second alone possesses gills, and narrow slits, with a lung-like branchial sac on each side opening between hyoid and first branchial arches and supplied by branchial arteries; *A. cuchia*; *Monopterus* Lacép., 3 branch. arches and small gills, no branch. sac, East Ind. Arch. and Cont.; *Symbranchus* Bl., 4 branch. arches and large gills, trop. Amer. and E. Ind.

\* Ballowitz, *Das elect. Organ des afrikanischen Zitterwelses*. Jena 1899.



Sub-order 4. **APODES (ANGUILLIFORMES).** The Eels.

The premaxillaries small or absent, the maxillaries lateral, the body eel-like and without pelvics. Symplectic absent; operculum and palatine arch reduced; scales absent or feeble; pectoral arch not attached to skull; fins without spines, median fins if present confluent; no pseudobranch; tail protocercal; no pyloric caeca; no generative ducts. Air-bladder, when present, with a ductus pneumaticus.

The eels are spread over the f. ws. and seas of the trop. and temp. zones; some descend to the greatest depths. The young of some have a limited existence and are known as *Leptocephalus* (see below). Fossil *Anguilla* in chalk of Aix and Oeningen, *Anguilla*, *Sphagebranchus*, *Ophichthys* at Monte Bolca and *Urenchelys* S. Wood., with homocercal tail, from the chalk.

The breeding \* of the common eel was until a short time ago a mystery. During their sojourn in freshwater they do not develop reproductive organs, and it was not known how they originated. Aristotle thought that they came from the "entrails of the earth." It is now known, thanks to the researches of Grassi and Calandruccio, that they breed in the depths of the sea, that the eggs float but remain near the bottom, and that they hatch out as a larva, which soon becomes transformed into a ribbon-shaped, transparent creature, which has long been known and called *Leptocephalus*. There are several kinds of *Leptocephalus*. That of the common eel is *L. brevirostris*. It appears to remain at the bottom, probably hiding under stones or burrowing in sand and mud until it metamorphoses into the elver. Elvers (see below) are the young of eels which ascend rivers in great numbers.

The Italian naturalists worked at Catania in the Straits of Messina, where specimens of the *Leptocephalus brevirostris* are common in certain years at the surface, and at all times in the stomach of *Orthogoriscus mola*, a deep-sea fish, and they showed that this particular kind is the larva of the common eel. That it should be taken here and nowhere else is a curious fact, considering that the common eel is widely distributed. The probable explanation is that it is brought to the surface by the currents and whirlpools which abound in this locality, while elsewhere it has escaped observation by lurking at considerable depths (300 fms.) in mud and under stones. Several species of *Leptocephalus*, which doubtless belong to different *Muraenidae*, are known as pelagic forms, especially in the tropics, so that it is probable that all *Leptocephali* are not confined to deep water during their development. Speaking generally it appears that female Muraenoids cannot mature their ova except in deep water, while the male can

\* B. Grassi and S. Calandruccio, Ulteriori ricerche sulle metamorfosi dei Murenoidi, *Rend. Acc. Lincei* (5), vi., p. 43, 1897; also *Q. J. M. S.*, 39, 1897, p. 371, and *Proc. Roy. Soc.*, 1896. Cunningham, *Journal of Marine Biological Assoc.* (2), 3, 1895, p. 278, and (2), 1, 1891, p. 16.



arrive at maturity at a less depth, but has to migrate to a greater depth to fertilise the eggs. The eggs float, but at a considerable depth and only exceptionally mount to the surface. The characteristics of typical *Leptocephali* are the transparent ribbon-shaped body with colourless blood, vent near the tip of the tail, small head, and large eyes.

It has long been suspected that certain *Leptocephali* were the larvae of the conger, but many held that they were abnormal overgrown larvae incapable of further development, on the ground that they attained a size larger than that of the youngest conger, and because of the great variability of their form and dentition. The first naturalist who definitely observed the metamorphosis of a *Leptocephalus* into a young conger was Delage in 1886 (*Comptes Rendus*, 103, 1886, p. 698). In this metamorphosis the skin became pigmented, the blood coloured, the air-bladder developed, and the body cylindrical and shorter.

Grassi has shown that *L. stenops* (in part), *L. morrisii* and *punctatus* belong to the life-cycle of *Conger vulgaris*; that *L. haeckeli*, *yarrelli*, *bibroni*, *gegenbaurii*, *köllikeri*, *stenops* (in part) belong to *Congromuraena mystax*; *L. taenia*, *inornatus*, and *diaphanus* to *Congromuraena balearica*, etc.

Fam. 21. **Derichthyidae**. Body eel-like, from the abysses of the Atlantic; *Derichthys* Gill.

Fam. 22. **Muraenidae**, with the characters of the sub-order. (This family is now usually divided into several.)

Group 1. Eels in which the branchial openings in the pharynx are wide slits.

*Nemichthys* Rich., jaws produced into long slender bill, eyes large, with *Serrivomer*, *Spinivomer*, *Avocettina*, *Labichthys* are deep-sea (500–2,500 fms.) forms. *Anguilla* Cuv., eels, small scales imbedded in the skin, upper jaw not projecting beyond the lower; gill-openings narrow, at the base of the pectoral fins; dorsal fin some distance from head; they freely ascend rivers, descending to the sea for purposes of reproduction; f. w. and coasts of temp. and trop. zones, not yet found in S. Amer., W. coast of N. Amer. and W. Afr. *A. anguilla* L., the common Eur. and Brit. species, they descend rivers in the autumn and spawn in the deep sea; the larva is known as *Leptocephalus brevirostris*; the young eels are called *elvers*, and ascend rivers in incredible numbers in spring (April and May), overcoming all obstacles and even crossing land; such migrations are known as eel-fares (of which elver may be a corruption), they bury themselves in mud and become torpid in winter, do not develop their generative products in freshwater; the adult eels are said not to re-ascend rivers and to die soon after spawning.

In eels migrating down the rivers to the sea the reproductive organs are enlarged, and the skin has a silver colouration. The eyes also are enlarged. All these peculiarities are observed in the sexually mature forms taken from the deep water. Young elvers are not known of a less size than 5 cm., while the larva, *L. brevirostris* attains a length of 8 cm.

*Simenchelys* Gill, and *Ilyophis* Gilbert, are deep-sea eels; *Synphobranchus* Johns., gill-openings united into a longitudinal slit, deep-sea congers; *Conger* Kaup., congers or marine eels, scaleless (*Leptocephalus*, *Oxyurus*, *Helmictis*, are all said to have priority over *Conger*), *C. conger* L., prefers deep waters with rocky bottom, attains to 8 ft., almost cosmopolitan; allied genera are *Poeciloconger*, *Congromuraena*, *Uroconger*, *Heteroconger*; *Muraenesox* McClell., scaleless, trop. seas; *Nettastoma* Raf., scaleless, deep-sea, the leptocephalid form is *Hyoprurus*; *Sauren-*

*chelys* (*Chlopsis*), *Oxyconger*, *Hoplunnis*, *Neoconger*, all with superior or lateral nostrils, and *Myrus*, *Ahlia*, *Myrophis*, *Paramyrus*, *Chilorhinus*, *Muraenichthys* with nostrils in the upper lip, may be placed here. *Ophichthys* Gthr. (*Ophichthus*), nostrils labial, extremity of tail free, more than eighty species known, very numerous in trop. seas, formidable dentition in jaws and palate; *Sphagebranchus*, *Verma* *Letharchus*, *Myrichthys*, *Pisodonophis*, *Callechelys*, *Bascanichthys*, *Quassiremus*, *Mystriophis*, *Scytalichthys*, *Brachysomophis*, are other allied genera; *Moringua* Gray, E. Ind., Fiji, Japan.

Group 2. Eels in which the branchial openings in the pharynx are narrow slits.

*Muraena* Gthr., scaleless; teeth well developed; pectoral fins absent, are as abundantly represented in tropical and sub-tropical waters as is *Ophichthys*; more than eighty species; most of them with formidable teeth, attain a length of 8 ft. and attack man, most are highly coloured. *M. helena* L., the *muraena* of the ancient Romans, can be domesticated, will live in fresh-water, Mediterranean, etc.; other genera are *Gymnomuraena*, *Myroconger*, *Enchelycore*, *Pythonichthys*, *Rabula*, *Lycodontis*, *Echidna* Forster 1778, *Uropterygius*, *Channomuraena*.

The family **Saccopharyngidae** may be placed here. They are eel-like deep-sea (Atlantic) fishes with feeble muscular system, but little earthy matter in their bones, and branchial arches far behind the skull, without palato-pterygoid bar, narrow tail ending in filament, and with pedunculated appendages in place of the lateral line. *Saccopharynx*, *Gastrostomus*, *Eurypharynx*.

#### Sub-order 5. HAPLOMI (ESOCIFORMES). Pike-like fishes.

Soft-rayed fishes with the mesocoracoid wanting, the coracoids normally developed, and the post-temporal normally attached to the cranium. Parietal bones separated by the supra-occipital. Symplectic present, opercular bones well developed. Anterior vertebrae unmodified. Air-bladder with duct; pelvic fins abdominal, rarely absent. First ray of dorsal fin occasionally stiffened and spine-like; no adipose fin. Chiefly f. w.

Fam. 24. **Galaxiidae**. Naked, without barbels; margin of upper jaw chiefly formed by premaxillaries. Dorsal fin opposite anal; pseudobranch absent. Without adipose fin; with air-bladder. Ova dehiscent into abdomen. F. w. and seas of temperate parts of S. hemisphere (S. Afr., Patagonia, N. Zealand, Tasmania), some are katadromous; *Galaxias* Cuv.

Fam. 25. **Haplochitonidae**, representing the salmonoids in the S. hemisphere. *Haplochiton* Jen.; *Prototroctes* Gthr.

Fam. 26. **Enchodontidae**. Extinct, Cretaceous. *Enchodus* Ag., etc.

Fam. 27. **Esocidae**. Body covered with scales; margin of upper jaw formed by premaxillaries and toothless maxillaries; barbels and adipose fin absent; unpaired fins far back; stomach without blind sac; pyloric caeca absent; pseudobranch glandular hidden; air-bladder simple; gill-opening very wide; noted for their voracity. *Esox* (L.) Cuv. (*Lucius* Raf.), the pikes, f. w. of temp. Eur., Asia and Amer.

*E. lucius* L., common pike, pickerel, jack, luce, hake, Eur., N. Asia and northern parts of North America; extremely voracious, does not refuse frogs, voles, house rats, puppies, kittens, weasels, foxes, ducks, geese, has been found with a human infant in its stomach, has been known to lay hold of a swan, a tame cormorant, and to attack otters, dogs, asses, mules, oxen, horses, men, and to catch swallows, dislikes sticklebacks. *Umbra* Kramer, Austria, Hungary (Hundsfisch), and United States (mud-minnow).

Fam. 28. **Dalliidae**, f. w. fishes from Alaska and Siberia.

Fam. 29. **Scopelidae**. Naked or scaly. Margin of upper jaw formed by premaxillary only; opercular bones thin but complete. Barbels none. Pseudobranchs usually well developed. Air-bladder small or none. Adipose fin present. The eggs are enclosed in the sacs of the ovary and are extruded by oviducts. Intestine short. All marine, mostly inhabiting shore waters, some descending to the deep sea. The following fossil forms are probably allied here: *Hemisaurida*, *Parascopelus*, *Anapterus*. *Saurus* Cuv., Med., trop. Atl. and Pac.; *Bathysaurus* Günth., deep sea, Pac., 1,100–2,400 fms.; *Harpodon* Les., Ind. and China Seas, *H. nehereus*, Bombay duck; *Scopelus* Cuv., lantern-fishes, luminous spots along sides of body, pelagic fishes, taken at any depth to 2,500 fms.; *Ipnops* Günth., 1,600 to 2,150 fms., phosphorescent organs extending along the median line of the snout, have been regarded as modified eyes, which are otherwise absent, pseudobranch absent; *Paralepis* Risso, small, pelagic, from Med. and Atl.; *Sudis* Raf.; *Plagyodus* Pall. (*Alepidosaurus* or *Alepisaurus* Lowe), one of the largest deep-sea fishes; other genera are *Aulopus*, *Chlorophthalmus*, *Scopelosaurus*, *Odontostomus*, *Nannobrachium*, *Bathypterois*; *Trachinocephalus* Gill, *Synodus* Bloch and Sch., *Benthosaurus* Goode and Bean; *Myctophum* Raf., pelagic fishes coming to surface at night, taken at any depth to 2,000 fms.

Fam. 30. **Cetomimidae**. *Rondeletia* Goode and Bean, deep sea; *Cetomimus*, Goode and Bean, deep sea.

Fam. 30 a **Chirothricidae**, extinct.

Fam. 31. **Kneriidae**. Small loach-like fishes from f. w. of trop. Africa. *Kneria*.

Fam 32. **Cyprinodontidae** (**Poeciliidae** J. and E.). Head and body covered with scales; barbels absent. Margin of upper jaw formed by premaxillaries only. Teeth in both jaws; upper and lower pharyngeals with cardiform teeth. Adipose fin absent; dorsal fin on the hinder half of the body. Stomach without blind sac; pyloric appendages absent. Pseudobranch absent; air-bladder simple. Sexes usually unlike, the fins being larger in the males, which however are often much smaller in size than the females; mostly viviparous, the young being well developed at birth. The anal fin of the male is frequently modified as a copulatory organ. Freshwater fishes of S. Eur., Asia, Afr. and Amer., some of them occurring in arms of the sea. Some are carnivorous and some live on organic substances in mud. Fossil remains in tertiary strata.

I. **Carnivorae**. Bones of each ramus of the mandible firmly united, intestine short or but little convoluted; carnivorous. *Cyprinodon* Lacép., in Mediterranean region and N. Amer., are able to live in brine pools, e.g., of Dead Sea and Sahara, and at high temperatures; sometimes lose their ventral fins and then known as *Tellia*; oviparous. Allied are *Fitzroyia* from Monte Video, and

*Characodon* from Central Amer. *Haphlochilus* M'Cl., E. Ind. trop. Afr., temp. and tropical Amer. *Fundulus* C. et V., killifish, abundant in New World, one in Spain and one in E. Afr.; allied are the South American *Limnurgus*, *Lucania*, *Rivulus* and *Cynolebias*; *Orestias* C. et V., East Peru and Bolivia, at an elevation of 13,000 to 14,000 ft.; *Jenynsia* Gthr., Madonado; *Gambusia* Poey, W. Indies, and S. Amer.; allied are *Pseudoxiphophorus* and *Belonesox* of Cent. Amer.; *Anableps* Art., four-eyed fishes, iris with two pupils, swims with part of head out of water, trop. Amer.

II. **Limnophagae.** Mandibular bones but loosely joined, intestine convoluted, sexes differentiated, mud-eating, trop. Amer. *Poecilia*, *Mollienesis*, *Platypoecilus*, *Girardinus*.

Fam. 33. **Amblyopsidae (Heteropygii).** Head naked, body with very small scales, barbels absent. Villiform teeth in jaws and on palate. Adipose fin absent. Pelvic fins small or absent. Vent in front of pectorals. Stomach caecal; pyloric caeca present. Pseudobranch absent (concealed). Fishes of small size living in the swamps and subterranean streams of the United States. *Amblyopsis* De Kay, the blind fish of the Mammoth Cave of Kentucky, colourless, 5 inches, eyes and optic nerve very imperfect\*; viviparous; allied species without pelvic fins are known as *Typhlichthys* Gerard. *Chologaster* Ag., with normal eyes and coloured; swamps and entering caves.

Fam. 34. **Stephanoberycidae**, deep sea.

Fam. 35. **Percopsidae.** F. w. of N. Amer.; adipose fin present; dorsal and anal with a few spines, pelvics abdominal with more than five soft rays, with a trace of pneumatic duct and with pseudo-branch; body covered with ctenoid scales. *Percopsis* Ag., *Columbia* Eigenm.

## Sub-order 6. HETEROMI (DERCETIFORMES).

Air-bladder without open duct; parietals separating the frontals from the supraoccipital; no mesocoracoid. Pelvics abdominal if present.

Fam. 36. **Dercetidae.** Eel-shaped fishes without ordinary scales. Body generally with four series of subtriangular scutes and intermediate scale-like smaller scutes. Head long and jaws produced. Extinct, Cretaceous. *Dercetis* Ag., *Pelargorhynchus* v. d. Marck.

Fam. 37. **Halosauridae**, deep-sea forms. *Halosaurus*, *Aldrovandia*.

Fam. 38. **Notacanthidae**, deep-sea, pelvics abdominal, air-bladder with duct. *Notacanthus*, *Macdonaldia*.

Fam. 39. **Lipogeniidae.** Deep-sea.

Fam. 40. **Fierasferidae**.† Without pelvic fins, vent at the throat; eel-like, small, shore-fishes of tropical seas, often living as lodgers in cavities of other animals, e.g. Holothurians, starfishes and bivalve molluscs; often commensal with the pearl oyster; are harmless to their hosts. *Fierasfer* Cuv., *Encheliophis*. *Lycodapus* Gilbert may be placed near here.

\* Eigenmann, *Arch. f. Entwickl. Mech.*, 8, 1899, p. 545.

† Emery, *Fauna und Flora d. Golf. v. Neapel*, 1880.



Sub-order 7. **CATOSTEOMI (GASTROSTEIFORMES).**

Air-bladder, if present, without open duct. Parietals, if present, separated by supraoccipital. No mesocoracoid. Ventral fins abdominal if present. Mouth bordered by the premaxillaries or by them and a small portion of the maxillaries.

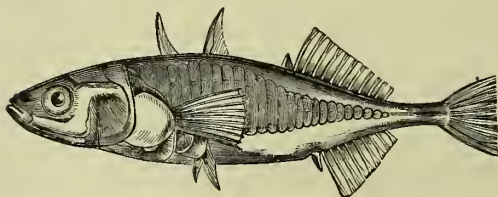


FIG. 124.—*Gasterosteus aculeatus* (after Heckel and Kner, from Claus).

**A. SELENICHTHYES**

Preoperculum and symplectic distinct; branchial apparatus fully developed; mouth terminal, toothless; post-temporal forked, free; pelvic bones connected with the scapular arch; pelvis with fifteen to seventeen rays; ribs long, sessile; fins without spines.

**Fam. 41. Lamprididae.**

Body short and deep, with minute scales. *Lampris* Retzius; *L. luna* Gmelin, the opah or king-fish, to 4 ft., N. Atl. and Med.

**B. HEMIBRANCHII.**

Gills pectinate. Post-temporal furcate. Superior pharyngeal bones reduced in number, the bones of the gill-arches also reduced except in *Gasterosteidae*; inferior pharyngeal bones present, not united. Pelvic fins abdominal. Mouth bounded above by premaxillaries only. Basis of cranium simple and without tube. Mouth small, at the end of the snout which is usually produced.

**Fam. 42. Gasterosteidae.**

Sticklebacks. Body elongate, compressed, cleft of the mouth oblique, villiform teeth in the jaws. Opercular bones not armed. Scales none, but generally large scutes along the side. Isolated spines in

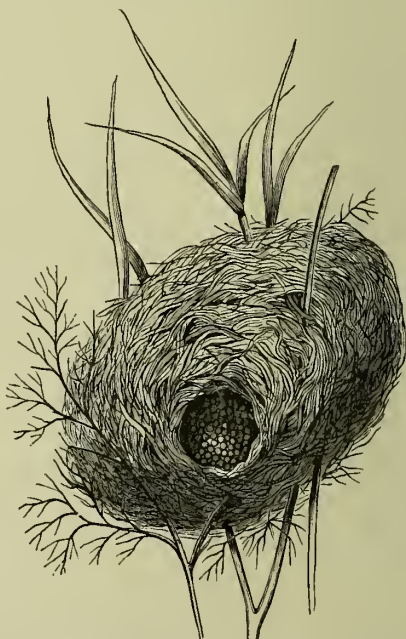


FIG. 125.—Nest of *Gasterosteus pungitius* (from Claus after Landois).



front of the soft dorsal fin. Pelvics abdominal, joined to the scapular arch. Branchiostegals 3. Pseudobranch and air-bladder present. Small fishes inhabiting f. w. and arms of the sea in Eur., As. and Amer.; noted for their pugnacity; they are very destructive to the spawn and fry of other fishes. In many species the males build nests for the eggs with blades of grass, etc., cemented together by cutaneous mucus; the male defends the eggs. They are extremely variable and susceptible to change of conditions. *Gasterosteus* Artedi, probably only 3 Brit. species, though many varieties have been described as such, *G. aculeatus*, the 3-spined, f. w., *G. pungitius*, the 9-spined, f. w., and *G. spinachia*, the marine stickleback; *Eucalia* Jordan, *Pygosteus* Brevoort, *Apeltes* De Kay; *Aulorhynchus* Gill.

Fam. 43. **Protosyngnathidae**. Extinct.

Fam. 44. **Fistulariidae**. Gigantic marine sticklebacks, flute-mouths, pipe-fishes, trop. and sub-trop. Atl. and Indo-Pac. *Fistularia*, *Aulostoma*, *Auliscops*.

Fam. 45. **Macrorhamphosidae**. Bones of the skull much prolonged anteriorly forming a long tube which bears the short jaws at its end; two dorsal fins, the spinous short; pelvics truly abdominal, imperfectly developed; the 4 anterior vertebrae much elongated. *Macrorhamphosus* Lac. (*Centricus* Cuv.), snipe fishes, *M. scolopax* L., the trumpet or bellows-fish, rarely occurs on S. coast of England; *Amphisila* Klein, body so thin as to be semi-transparent, trunk part of vertebral column composed of 6 vertebrae, and four times as long as the caudal, which consists of 14, with a dorsal cuirass formed by portions of the skeleton.

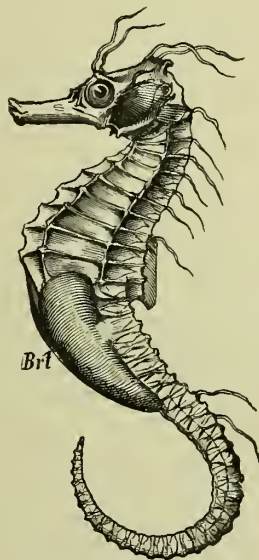


FIG. 126—Male of *Hippocampus* with the brood-pouch. Br. (from Claus).

### C. LOPHOBRANCHII.

Gills composed of small rounded lobes attached to the branchial arches; gill-cover a large simple plate; air-bladder simple, usually without duct (present in *Syngnathus acus*); skin with bony plates; muscular system feeble; snout prolonged, bearing the small terminal toothless mouth, bounded above by premaxillaries only; scapula attached to skull by post-temporal; bad swimmers, carried about by currents.

Fam. 46. **Solenostomidae**. Gill-openings wide, two dorsal fins, the rays of the anterior not articulated; all the other fins well developed; in the female the eggs are retained in a brood pouch formed by the broad pelvic fins. *Solenostoma* Lac., Ind. Ocean, preceded in the tertiary epoch by *Solenorhynchus*.

Fam. 47. **Syngnathidae**. Gill-openings very small, near the upper posterior angle of the gill-cover; one soft dorsal fin; no pelvics; males with an egg-pouch placed on the ventral side of the tail or abdomen usually formed of two folds of skin; eggs are retained here till some time after hatching; small fishes found in all warm seas, sometimes entering f. w.

A. Tail not prehensile, generally with caudal fin. Pipe-fishes. *Siphonostoma* Kaup; *S. typhle* L. coasts of Eur. *Syngnathus* Art.; *S. acus* L. greater pipe-fish. *Doryichthys*. *Nerophis* Kaup., eggs glued to abdomen, no folds of skin; *N. aequoreus* L. ocean pipe-fish, *N. ophidion* L. straight-nosed pipe-fish, *N. lumbriciformis* Yarr. little pipe-fish common on British coasts; *Protocampus*, *Ichthyocampus*, *Nannocampus*, *Urocampus*, *Leptoichthys*, *Coelonotus*, *Stigmatophora*.

B. Tail prehensile, without caudal fin. Sea-horses. *Gastrotekeus*, *Solenognathus*. *Phyllopteryx* Swainson, provided with prominent spines on the edge of the body, some with cutaneous filaments giving them a close resemblance to the seaweed which they frequent; *Hippocampus* Raf., sea-horse (Fig. 126), *H. antiquorum* Leach, Brit. seas, etc.

#### D. HYPOSTOMIDES.

With one Fam. 48. **Pegasidae**, Body entirely covered with bony plates; preoperculum and symplectic absent; the pectorals are broad

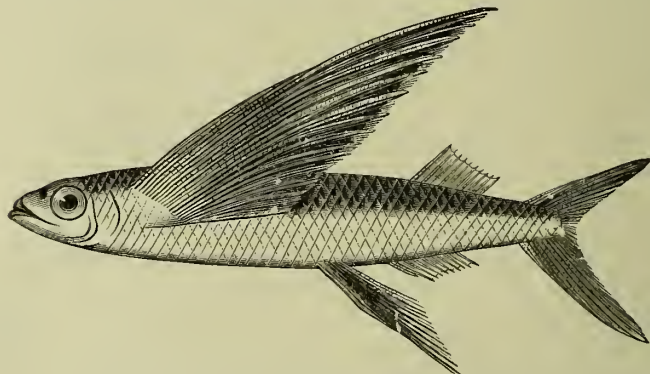


FIG. 127.—*Exocoetus rostratus* (after Cuv. and Vah., from Claus).

and horizontal; and the upper part of the snout is produced into a process; without air-bladder and pseudo branch. Small fishes living in sandy shoal-places near the coast. Indian Ocean, Chinese and Australian coasts. *Pegasus draco* and *volans*.

#### Suborder 8. **PERCESOCES (MUGILIFORMES).**

Air-bladder, if present, without open duct. Parietals separated by supraoccipital. Pectoral arch suspended from skull, no mesocoracoid. Pelvic fins, if present, often with 1 spine and 5 rays; pelvic bones not attached to shoulder girdle. Connects the Haplomi with the Acanthopterygii.

Fam. 49. **Scombresocidae**. Body covered with scales; a series

of keeled scales along each side of the belly; maxillae entering border of upper jaw; lower pharyngeals united into a single bone; no adipose fin; pelvics without spines, with 6 rays; air-bladder generally present without duct; pseudobranch hidden glandular; stomach not distinct from intestine, which is quite straight, without appendages. Chiefly marine, but some acclimatised in f. w.; many of the latter are viviparous. All trop. and temp. zones (*Holosteus* in the strata of Monte Bolca is allied here). *Belone* Cuv., with green bones, both jaws elongated into a beak, no finlets; *B. vulgaris* Flem., Brit. coast, gar-fish, gar-pipe, sword-fish. *Scombrox* Lac., the saury or skipper, both jaws elongated into a beak, finlets behind anal and dorsal fins; *S. saurus* Rond., Brit. coast. *Tylosurus*, *Athlennes*, *Hemirhamphus*, *Arrhamphus*, *Chriodorus*, *Hyporhamphus*; *Ecoetetus* Art., flying fish (Fig. 127), both jaws short, pectoral fins elongated into organs for floating through the air (parachute-like), they live in shoals in trop. and sub-trop. seas, *E. volitans* L., has been taken off Brit. coast; flying fish do not fly, but leaving the water by a powerful tail movement they float rapidly through the air in a straight line supported by their expanded pectoral fins. *Fodiator*, *Parexocoetus*, *Halocyclus*.

Fam. 50. **Ammodytidae**. Sand-eels. Small carnivorous fishes swimming in shoals near the shore and burying themselves in the sand; pelvics absent; vent remote from head, long dorsal and anal fins destitute of spines; pelvics without spine, with 6 rays; no air-bladder. *Ammodytes* L., *A. lanceolatus*, greater sand-eel; *A. tobianus*, lesser sand-eel.

Fam. 51. **Atherinidae**. Lateral line indistinct, with a silvery band along the sides; valued as food; the fossil *Mesogaster* allied here. *Atherina* L., littoral fishes living in shoals, like smelts; the newly hatched young are called nonnat in S. France. *A. presbyter* Jenyns, silverside, and *A. boyeri* are British; *Lethostole* J. and E.; *Chirostoma* Swains. (*Atherinichthys* Bleek), pesce rey; *Kirtlandia*; *Menidia*; *Leuresthes*; *Eurystole*; *Thyrina*; *Atherinella*; *Labidesthes*; *Atherinopsis*; *Atherinops*.

Fam. 52. **Mugilidae**. Grey mullets. Lateral line absent; large cycloid scales; anterior dorsal of 4 stiff spines. *Mugil* L., grey mullets, stomach muscular in part, like gizzard of fowl, feed on mud and sand, and have long gill-rakers, along shores and in brackish lagoons, intestine much convoluted and long, *M. capito* Cuv. grey mullet, and *M. chelo* Cuv. lesser grey mullet, are British; *Chaenomugil*, *Querimana*, *Agonostomus*, *Joturus*.

Fam. 53. **Sphyrænidae**. Barracudas. Lateral line continuous, small cycloid scales; carnivorous pike-like fishes, often of large size, inhabiting warm seas, many used as food; *Sphyræna* Bl. and Schn.

Fam. 54. **Polynemidae** with *Polynemus*, *Pentanemus*, *Galeoides*, *Polydactylus*; flesh esteemed, air-bladder yields isinglass, humeral arch with long filaments, sandy shores of trop. seas sometimes entering rivers.

Fam. 55. **Chiasmodontidae**. Deep-sea; *Chiasmodon* Johnson or *Chiasmodus* Gthr., *Pseudoscopelus* Lütken.

Fam. 56. **Stromateidae**, Pelagic or deep-sea fishes, with *Nomeus*, *Cubiceps*, *Psenes*, *Seriola*, *Psenopsis*, *Centrolophus*, *Lirus*, *Stromateus*, *Peprillus*, *Stromateoides*.

Fam. 57. **Tetragonuridae**. *Tetragonurus*, a rare fish from Mediterranean, Atlantic and S. Pacific, poisonous as food.

Fam. 57a. **Icesteidae**. *Ichthyus*, *Icesteus*, *Acrotus*, all deep-sea.

Fam. 58. **Ophiocephalidae**. Fresh-water fishes of the Indian region

and trop. Africa; they are able to survive drought in semi-fluid or beneath dry mud, and have an accessory branchial cavity for aerial respiration; maxillae excluded from border of upper jaw; head and body covered with cycloid scales; pectorals nearer ventral than dorsal line; pelvics if present near pectoral, with 6 rays; dorsal and anal fins long, without spines; air-bladder long. *Ophiocephalus*, *Channa*.

Fam. 59. **Anabantidae**. Closely related to preceding, but differ in part of the dorsal and anal fins, and the outer ray of the pelvic being spinous. The accessory suprabranchial organ is more developed with thin bony laminae which are more or less folded; f. w. fishes of India, Malay Pen. and Arch., and Africa. One genus, *Anabas* Cuv.; *A. scandens* Dald., climbing perch, Ind. region, can move on land, and has been taken ascending a tree (five feet up) by means of its pre-opercular and anal fin spines.

### Sub-order 9. ANACANTHINI (GADIFORMES).

Median and pelvic fins without spinous rays; the pelvics when present are jugular or thoracic. Air-bladder, if present, without duct. Parietals separated by the supraoccipital. Pectoral arch suspended from the skull; no mesocoracoid. Caudal fin, if present, without expanded hypural, perfectly symmetrical and supported by the neural and haemal spines of the posterior vertebrae and by basal bones similar to those supporting the dorsal and anal rays; the ventral part of the caudal fin is not a true caudal, but an anal shifted back to the end of the body; according to this view the condition in the Macruridae must be more primitive than that in the Gadidae.

Fam. 60. **Macruridae**. Body ending in a long compressed tapering tail without caudal fin; covered with spiny, keeled or striated scales; one short anterior dorsal and a long posterior dorsal meeting the long anal at the end of the tail; deep-sea forms. *Bathygadus*, *Macrurus*, *Coryphaenoides*, *Macruronus*, *Malacocephalus*, *Moseleya*, *Lionurus*, *Lyconus*, *Gadomus*, *Melanobanchus*, *Trachyrhynchus*, *Hymenocephalus*, *Steindachneria*.

Fam 61. **Gadidae**. Cod-fishes. More or less elongate, covered with small smooth scales; 1, 2 or 3 dorsal fins, 1 or 2 anals; caudal distinct or confluent with the dorsal and anal, symmetrical, the ventral part of it having interspinous bones; gill-opening wide; gill-membrane usually not attached to isthmus; pseudobranch absent or glandular; air-bladder and pyloric caeca generally present; gills 4, a slit behind the 4th; genera about 25; many highly valued as food, chiefly in the northern seas, littoral, surface or abyssal; one genus (*Lota*) is f. w.; some marine members of the family will live in f. w. lakes close to the sea. *Gadus* Art. Arctic and temp. zones of the n. hemisphere. *G. morrhua* L. the cod, *G. aeglefinus* L. the haddock, *G. luscus* L. bib or whiting pout, *G. minutus* L. the power, *G. merlangus* L. whiting, *G. pontassou* Risso, *G. pollachius* L. pollack; *Gadiculus*, *Mora*, *Strinsia*; *Halargyreus* and *Melanonus* are bathy-



bial. *Merluccius* Cuv. *M. vulgaris* Flem. hake; *Pseudophycis*, *Lotella*, *Physiculus*, *Uraleptus*, *Laemonema*; *Phycis* Bl. Sch., *Ph. blennioides* Bl. Sch.; *Haloporphyrus* (*Lepidion*) and *Antimora* abyssal; *Lota* Cuv. f. w., *L. vulgaris* Cuv., the burbot or eel pout, in some English rivers; *Molva* Nilss. *M. vulgaris* Flem. the ling; *Motella* Cuv., rock-lings; *M. mustela* Nilss., *M. cimbria* Nilss., *M. tricirrata* Nilss., *M. macrophthalma* Gthr.; *Raniceps* Cuv., *R. raninus*; *Bregmaceros*; *Brosmius* Cuv., *B. brosme* the torsk; *Theragra*, *Eleginus* Fischer. *Muraenolepis* without separate caudal fin may be placed here.

### Sub-order 10. ACANTHOPTERYGII. Spiny-rayed fishes.

Anterior vertebrae unmodified; anterior rays of dorsal and anal fins typically simple or spinous, but all the fin-rays are sometimes jointed. The lower pharyngeals are generally separate. Air-bladder if present typically without pneumatic duct in the adult. Border of upper jaw formed by premaxillary. Supraoccipital in contact with frontals. Shoulder girdle attached to skull by post-temporal. No mesocoracoid. Opercular apparatus complete; gill-openings in front of the pectorals. Pelvic fins more or less anterior, normally attached to the shoulder-girdle, typically with 1 spine and 5 rays. The great majority of marine fishes belong to this section. They differ widely among themselves and some of them approach closely to the sub-orders previously described. A certain number of the tribes can be clearly defined, but many of them include forms so diverse that they defy concise definition, and can only be described as centres of relationship.

#### Tribe 1. PERCIFORMES, Perch-like fishes.

No bony stay for the prooperculum. Basis cranii double. Spinous dorsal usually well developed. Pectoral arch with well-developed scapula and coracoid, the former pierced by a foramen or fenestra; somactids longer than broad, more or less hour-glass shaped, four or five in number, one or two of which are in contact with the coracoid. Pelvics thoracic. Rays of the caudal fin not strongly forked at the base, hypural usually with a basal spine or knob-like process on each side.

This group is incapable of concise definition. It includes fishes of divers habits and forms. "The division into families, capable of rigid definition is a task of considerable difficulty, and the necessities of a linear arrangement result in the breaking up of some natural sequences." \*

Fam. 62. **Berycidae**. Body compressed, covered with cycloid or etenoid scales; head with large muciferous cavities covered by the skin; pelvics thoracic, with one spine and more than five soft rays; with pseudo-branch and numerous pyloric caeca; air-bladder with pneumatic duct in *Beryx* and *Holocentrum*; mostly deep-sea fishes, many extinct species.

\* Boulenger, in *Cambridge Natural History*.



*Beryx* Cuv., with large ctenoid scales, air-bladder with duct, deep-sea, is found fossil in the chalk; *Polymixia*, *Aphredoderus*, *Plectromus*, *Scopelogadus*, *Anoplogaster*, *Caulolepis*, *Trachichthys*, *Gephyroberyx*, *Myripristis*, *Holocentrum*.

Fam. 63. **Monocentridae** with *Monocentris*.

Fam. 64. **Pempheridae**, *Pempheris*, air-bladder divided into an anterior and posterior portion; *Bathyclupea* Alcock, with pneumatic duct.

Fam. 65. **Cyphosidae**. Pacific and Indian Oceans. *Cyphosus* Lac. (*Pimblepterus* Lac.), *Hermosilla*, *Sectator*.

Fam. 66. **Lobotidae**. *Medialuna*, *Lobotes*, very wide range.

Fam. 67. **Centrarchidae**. Sun-fishes, f. w. of N. Amer., most build nests, valued as food. *Pomoxis*, *Centrarchus*, *Acantharchus*, *Ambloplites*, *Archoplites*, *Chaenobryttus*, *Enneacanthus*, *Mesogonistius*, *Apomotis*, *Lepomis*, *Eupomotis*, *Micropterus* Lac. (*Huro* C. and V.), black bass, acclimatised in Eur., *Elassoma*, *Kuhlia*.

Fam. 68. **Toxotidae**. *Toxotes* Cuv., f. w. and coasts of E. Indies and Australia, has the habit of throwing a drop of water at an insect near the surface to make it fall in.

Fam. 69. **Nandidae**. Small carnivorous fresh-water fish from W. Afr., S.-E. Asia and S. Amer. *Nandus*.

Fam. 70. **Percidae**. No sub-ocular lamina of the suborbitals; entopterygoid present; anterior vertebrae without transverse processes all or most of the ribs inserted on to the transverse processes; two nostrils on each side; gill membranes free from the isthmus; 6-8 branchiostegals; gills 4, a slit behind the 4th; pseudobranch variously developed, rarely absent; pharyngeal bones separate; soft portion of dorsal fin not much more developed than anal; latter with 1 or 2 spines. F. w. fishes of temp. N. hemisphere. *Perca* Art. Eur. C. and N. Asia, E.N. Amer.; *P. fluviatilis* Rond., the perch. *Lucioperca* Cuv., pike-perches; *Percina* (*Pileoma*); *Etheostoma* Raf., darters, N. Amer., E. of Rockies; also from E. of N. Amer. are *Bolcosoma*, *Ulocentra*, *Diplesium*, *Ammocrypta*, *Crystallaria*; *Aspro* C. and V. (*Zingel*), Cent. Eur.; *Percarina* Nord., rivers discharging into Black Sea and Sea of Azov; *Acerina*, Eur. and N. Asia, *A. cernua* L., the pope.

Fam. 71. **Cheilodipteridae**. Cardinal-fishes; small fishes of the tropics, abundant in the E. Ind., some f. w., some mar.; colour often bright red. *Ambassis* Commers., the smallest Percoids, some not much more than 1 in., trop. Indo-Pac. and f. w. of that area. *Apogon* Lac., coral-fishes, on or near coral reefs, a few enter f. w.; *Apogonichthys*, *Chilodipterus*, *Acropoma*, *Scombrops*, *Glossamia*, *Epigonus*, *Amiichthys*, *Hypoclydonia*; *Pomatomus* Risso, Med. and Atl. deep-water.

Fam. 72. **Serranidae**. Sea-bass. Second sub-orbital with an internal lamina supporting the globe of the eye; entopterygoid present. Anterior vertebrae without transverse processes; all or most of the ribs inserted on the transverse processes where these are developed. Two nostrils on each side; 6 or 7 branchiostegals; anterior vertebrae, ribs, gill membranes, nostrils, gills, pseudobranch, pharyngeal bones (except *Centrogenys*, in which they are united), dorsal fin as in *Percidae*. Carnivorous fish, chiefly mar., found in all warm seas and some in f. w. One of the largest families of fishes, about 550 species; *Percichthys* Gir. f. w. of Chili, W. Argentina, Patagonia; *Percilia* Gir., f. w., Chili; *Latcolabrax* Bleek, and *Nippon* C. and V., coasts China and Japan;

*Morone* Mitch. (*Labrax* C. and V.), Atl., f. w. of N. Amer., Med.; *M. lupus*, bass; *Percalates* Ram. and D.-O., f. w. and river mouths of S.-E. Australia; *Ctenolates* Gthr., and *Macquaria* C. and V., rivers S.-E. Australia; *Siniperca* Gill, rivers of China, Manchuria and Jap.; *Acanthistius* Gill, S. Pac. and S. Atl.; *Pomodon* Blgr., coasts Chili and Peru; *Parascorpius* Bleek, coasts S. Afr.; *Trachypoma* Gthr., S. Pac.; *Centrogenys* Rich., Ind. and W. Pac. Oceans. *Polyprion* Cuv., Atl. and Pac., mostly at great depths, to 80 lb. or more; *P. americanus* Bl. Schn. (*cernium* Val.), the stone-bass, excellent eating, has the habit of accompanying floating wood for the food on it; *P. (Oligorus) gigas*, the hapaku, coast of N. Zealand, also good eating; *Oligorus* Gthr., *O. macquariensis* Othr., murray-cod, Australian rivers, good eating; *Stereolepis* Ayres, coasts Jap. and California; *Dinoperca* Blgr., coasts of Baluchistan, S. Afr., Sind; *Liopropoma* Gill, coasts of Cuba, Jap. and Mascarene Islands; *Aulacocephalus*, *Gonioplectrus*, *Plectropoma*; *Epinephelus* Bl. (*Plectropoma*), a large number of species from temp. and trop. seas; *Anhyperodon*, *Cromileptes*, *Paranthias*. *Serranus* Cuv., sea-perches, coasts of Eur., Afr. and Amer., a few enter brackish and fresh-water; several of the species (*S. cabrilla*, *scriba*, *hepatus*) are normally hermaphrodite, distinction of species difficult, great variation with age, most are edible; *S. cabrilla* L. is Brit. *Centropristis*, *Gilbertia*, *Colpognathus* Klunz. (*Plectropoma*), *Caesioperca* Casteln. (*Anthias*), *Caprodon* Temm. and Schleg. (*Anthias*), *Holanthias* Gthr. (*Anthias*), *Odontanthias*, *Anthias*, *Plectranthias*, *Dactylanthias*, *Callanthias*, *Plesiops*, *Trachinops*, *Pogonoperca*, *Grammistes*, *Rhypticus*, *Priacanthus*. Lates C. and V., *L. niloticus*, the perch of the Nile; *L. calcarifer*, the perch of the Ganges, cockup; *Centropomus*, *Psammoperca*.

Fam. 73. **Pseudochromidae**. Marine perches of small size in the Atl., Ind. and Pac. Oceans. *Opisthognathus*, *Pseudochromis*, *Cichlops*, *Latilus*, *Caulolatilus*, *Lopholatilus*, *Malacanthus*, *Bathymaster*, *Rathbunella*.

Fam. 74. **Cepolidae**. Band-fishes, marine. *Cepola rubescens* is British.

Fam. 75. **Hoplognathidae**. Bones of the jaws with a sharp denticerous edge; Australian, Japanese and Peruvian coasts. One genus *Hoplognathus*.

Fam. 76. **Sillaginidae**. Small plain-coloured shore fishes common in Indian Ocean to coasts of Australia. *Sillago*.

Fam. 77. **Sciaenidae**. Found on sandy shores in all warm seas, a few species confined to f. w.; many attain a large size, most are edible and make a peculiar grunting or drumming noise; air-bladder frequently with numerous appendages. *Pogonias* Cuv.; *P. chromis* L., the drum; *Micropogon*, *Umbrina*, *Sciaena*, *Pachyurus*, *Otolithus*, *Cynoscion*, *Ancylodon*, *Collechthys*, *Larimus*, *Eques*, *Nebris*, *Lonchurus*, *Corvula*, *Bairdiella*, *Ophioscion*, *Stellifer*, *Menticirrhus*.

Fam. 78. **Cirrhitidae**. Carnivorous fishes of the warm seas, allied to *Serranidae* and *Scorpaenidae*. *Chilodactylus*, *Mendosoma*, *Nemadactylus*. *Latris* Rich., Tasmania and N. Zealand, among the most important food fishes of the S. hemisphere; *L. hecateia* Rich., the trumpet, 30 to 60 lb., and *L. ciliaris* Forst. to 20 lb.; *Chironemus*, *Cirrhitus*.

Fam. 79. **Lutianidae**. Edible, shores of warm regions. *Hoplogragnus*, *Evoplites*, *Neomaenis* Gir., snappers; *Apsilus*, *Etelis*, *Verilus*, *Xenocys*, *Nemipterus* (*Synagris*).

Fam. 80. **Haemulidae**. Carnivorous fishes of the warm seas, mostly

edible. *Haemulon*, *Anisotremus*, *Conodon*, *Pomadasis* (*Pristipoma*), *Orthopristis*, *Diagramma*.

Fam. 81. **Sparidae**. Sea-breams. Carnivorous shore-fishes of trop. and temp. seas, mostly edible; *Sparnodus*, *Sargodon*, *Capitodus*, *Soricidens*, *Asima* are extinct forms from Eocene and Miocene.

**Cantharina** without molar or vomerine teeth. *Cantharus* Cuv.; *C. lineatus* Mont., black-sea bream, old-wife; *Box*, *Scatharus*, *Oblata* from Med. and adjacent Atl.; *Crenidens*, *Tripteron*, Ind. Oc.; *Pachymetopon*, *Dipterodon*, *Gymnocrotaphus* from the Cape; *Girella*, *Tepraecops* from Chinese and Australian seas; *Doydixodon* from Coasts of Peru.

**Haplodactylina**, without molar with vomerine teeth. *Haplodactylus*, from temp. S. Pac..

**Sargina**, with a single series of incisors, and several series of rounded molars. *Sargus* Cuv. (*Diplodus* Raf., *Archosargus* Gill.); sargo, sar, saragu; several species in Med. and adjacent Atl.; *S. ovis* Mitch., sheep's head, from coasts of U. S.; *Otrynter*.

**Pagrina**, with single series of conical teeth in front, and molars at the sides. *Lethrinus* Cuv., trop. Indo-Pac., and one species on W. coast Afr., *Sphaerodon*; *Pagrus* Cuv. warmer temp. seas; *Stenotomus* Gill., *St. argyrops*, scup, porgy; *Pagellus* C. and V., *P. centrodonatus* De la R., sea-bream, chad; *Chrysophrys* Cuv., trop. and warm temp. seas. *Ch. aurata* L., gilt-head; *Calamus* Swains., Amer. coasts.

Fam. 82. **Maenidae**. Carnivorous shore-fishes. *Maena*, *Smaris*, *Caesio*, *Erythrichthys*, *Spicara*, *Emmelichthys*.

Fam. 83. **Gerridae**. Trop. seas. *Gerres*, *Eucinostomus*, *Ulaema*, *Xystaema*.

Fam. 84. **Trichodontidae**. Teeth slender and sharp, in bands on jaws and on vomers, 4 holobranchs and large pseudobranch; North Pacific, living in sand near the shore. *Trichodon* Cuv., *Arctoscopus* J. and E.

Fam. 85. **Mullidae**. Red mullets, slightly compressed, covered with large thin scales which may be ctenoid; two long erectile barbules on the hyoid; two short dorsals remote from each other; pelvics with 1 spine and 5 rays; branchiostegals 4; mainly tropical. *Mullus* L., highly prized as food; are skinned before death to produce expansion of the red chromatophores; *M. barbatus* L., Eur. species, *M. surmuletus* L., surmullet, is said to be the female of *barbatus*; *Mulloides*, *Upeneus*.

Fam. 86. **Caproidae**. Boar-fishes. In rather deep water; body compressed; mouth protractile; minute teeth on jaws and vomer; Mediterranean, Atlantic. *Capros*, *Antigonia*.

Fam. 87. **Chaetodontidae**, sometimes separated as a distinct tribe and divided into families, may also be placed here; the soft part of the unpaired fins and sometimes the spinous part are covered with small scales. The body is compressed and elevated and covered with scales either ctenoid or smooth; the limits of the group are uncertain; it includes forms showing analogies with the *Carangidae* on the one hand, and with the *Percoids* on the other, and there are features of specialisation which lead towards the *Plectognathi*. The majority are from tropical seas, and abound chiefly in the neighbourhood of coral reefs. The beauty and singularity of colouring of some of the genera, e.g. *Chaetodon*, *Heniochus*, *Holacanthus* are remarkable.

*Chaetodon* Art., many species from trop. Atl. and Indo-Pac.; *Chelmo* Cuv., with long slender bill; *Heniochus*, *Holacanthus*, *Pomacanthus*, *Scatophagus*, *Ephippus*, *Drepane*, *Scorpiis*, *Atypichthys*.

*Teuthis* L. (*Acanthurus* Forsk., young form *Acronurus*), *Naseus*, *Priognurus*, *Xesurus* J. and E., may be placed in the neighbourhood of the *Chaetodontidae*.

Fam. 88. **Osphromenidae**. Second suborbital with a more or less developed internal lamina; entopterygoid present; palate toothed. Two nostrils on each side; gills 4, a slit behind 4th; pseudobranch absent. Pelvics with not more than 5 soft rays. A superbranchial respiratory organ, placed in a cavity above the gills. F.w. fishes resembling the *Anabantidae*, and confined to S.E. Asia and Africa; 7 genera. *Polyacanthus* K. and v. H., E. Ind. Arch., beautiful colours, some species domesticated and several varieties produced, one called paradise-fish; *Osphromenus* Commers., *O. olfax* Commers., the gourami; *Betta* Bleek, *B. pugnax* Cant., pla-kat or fighting fish, very pugnacious; they are kept by the Siamese for fighting; when two are brought together or a single one sees its reflection in a glass, they become greatly excited and shine with a metallic lustre, and make repeated darts at each other. *Micracanthus*, *Trichogaster*, *Luciocephalus*, *Helostoma*.

Fam. 89. **Embiotocidae**. Viviparous fishes (eggs developing in a saccular enlargement of the oviduct), temp. N. Pacific. *Ditrema*, *Hysterocephalus*, *Cymatogaster*.

Fam. 90. **Cichlidae (Chromides)**. No subocular shelf; entopterygoid present; palate toothless; lower pharyngeal bones more or less completely united. A single nostril on each side. Gill-membranes free from the isthmus; 5 or 6 branchiostegal rays; gills 4, a slit behind the 4th; no pseudobranch. Dorsal fin more or less elongate, with numerous spines; anal with 3 spines or more; pelvics with 1 spine and 5 soft rays. F.w. or brackish water forms; variable in form and dentition. The eggs and young are cared for by the parents, male or female, which shelter them in the mouth. About 45 genera, Afr., Madagascar, Syria, India, C. and S. Amer. The fish-fauna of Lake Tanganyika is largely made up of this family. *Ectopplus*, *Chromis*, *Acara*, *Heros*, *Cichla*, etc.

Fam. 91. **Pomacentridae**. Marine fishes living chiefly near coral reefs, similar in mode of life to *Chaetodon*. *Pomacentrus*, *Amphiprion*, *Parma*, etc.

Fam. 92. **Labridae**. Wrasses. No subocular shelf, entopterygoid present, palate toothless; anterior teeth usually strong and canine-like; posterior teeth often soldered at the base; lower pharyngeals completely united into one bone with conical or tubercular teeth. Two nostrils on each side. Body covered with cycloid scales; one dorsal fin with the spinous portion as well developed as, or more than the soft; the soft anal similar to the soft dorsal; pelvics thoracic with 1 spine and 5 soft rays; branchiostegals 5 or 6; gills  $3\frac{1}{2}$ ; pseudobranch and air-bladder present; pyloric caeca and stomach caecum absent; 60 genera, temp. and trop. seas, diminishing towards Arctic and Antarctic circles, among rocks and kelp; often brilliantly coloured and valued as food fishes, are readily recognized by their thick lips. British genera are *Labrus* Art., *L. maculatus* Bl. ballan wrasse, *L. mixtus* L. striped wrasse or cook; *Crenilabrus* Cuv., *C. melops* L. gold-sinny or cork-wing; *Ctenolabrus* C. and V., *Ct. rupestris* L.; *Acantholabrus* C. and V.;



*Centrolabrus* Gthr. ; *C. exoletus* L., rock-cook ; *Coris* Lac., *C. julis* Gthr., rainbow wrasse. Other genera are

<i>Tautoga</i>	<i>Julis</i>	<i>Duymaeria</i>
<i>Lachnolaemus</i>	<i>Pseudodax</i>	<i>Cirrhitlabrus</i>
<i>Malacopterus</i>	<i>Choerops</i>	<i>Doratonotus</i>
<i>Cossyphus</i> (Harpe)	<i>Xiphochilus</i>	<i>Pseudochilinus</i>
<i>Chilinus</i>	<i>Semicossyphus</i>	<i>Hemigymnus</i>
<i>Epibulus</i>	<i>Trochocopus</i>	<i>Gomphosus</i>
<i>Anampses</i>	<i>Decodon</i>	<i>Cheilio</i>
<i>PlatyGLOSSUS</i>	<i>Pteragogus</i>	<i>Cymolutes</i>
<i>Iridio</i>	<i>Clepticus</i>	<i>Chlorichthys</i>
<i>Halichocres</i>	<i>Labrichthys</i>	<i>Xyrichthys</i>
<i>Novacula</i>	<i>Labroides</i>	<i>Miistius</i> .

*Odax* ; *Coridodax* Gthr. ; *C. pullux*, butter or kelp-fish of N. Zealand ; *Olistherops*, *Siphonognathus*.

Fam. 93. **Scaridae**. Parrot-wrasses, close to preceding. Jaws forming a sharp beak, the teeth being soldered together ; herbivorous fishes especially abundant among coral reefs. *Scarus* Forsk., *S. cretensis* L., Med., much esteemed as food by the Ancients ; *Scarichthys*, *Cryptotomus* (*Callyodon*), *Pseudoscarus*, *Calotomus*, *Sparisoma*.

#### Tribe 2. **SCOMBRIFORMES**. Mackerel-like fishes.

No bony stay for preoperculum. Spinous dorsal if distinct formed of short or feeble slender spines. Pectoral arch similar to Perciformes, but somactids more abbreviated. Pelvics thoracic ; caudal, if well developed, with numerous rays deeply forked at the base. This tribe is not capable of exact definition. It includes marine fishes, with few exceptions.

Fam. 94. **Scombridae**. Mackerels. Fusiform, naked or with small scales, eyes lateral, dentition well developed, two dorsal fins, generally finlets ; pelvics thoracic with 1 spine and 5 rays ; more than 10 abdominal, never more than 14 caudal vertebrae ; pseudobranch large ; air-bladder small or absent ; most pelagic, valued as food, and widespread ; their muscles receive a greater supply of blood and nerves than in other fishes, and are of a red colour, and their temperature is several degrees higher than in other fishes ; spawn in the open sea. Extinct forms in the Eocene and Miocene. *Scomber* L., *S. scomber* L., the common mackerel without air-bladder ; *S. pneumatophorus* with air-bladder ; *Auxis* C. et V. ; *A. rochei* Gthr. ; *Thynnus* Cuv. (*Thunnus*) (*Orcynus* Lütken), *Th. thynnus*, the tunny, one of the largest fishes, to 10 ft. ; *Th. pelamys*, the bonito, pursues flying fish ; some of the other species (? separate genus *Germo* Jordan) are provided with very long pectoral fins and are called by sailors "albacore." *Pelamys* C. et V. (*Sarda* Cuv.), *P. sarda* C. and V. ; *Cybium* Cuv. (*Scomberomorus* Lac.). *Acanthocybium* Gill ; *Rhachicentron* Kaup (*Elacate* C. et V.) may be placed here.

Fam. 95. **Gempylidae**. Fishes of the high seas, widespread, descending to considerable depths, usually breeding about rocky islands, most used as food. *Bipinnula* J. and E., *Ruvettus* Cocco, *Epinnula* Poey, *Nealotus* Johns., *Gempylus* C. et V.

Fam. 96. **Lepidopidae**. Transitional between muscular mackerel-



like fishes and band-shaped pelagic fishes with many vertebrae, *Aphanopus* Lowe, *Euoxymentopon* Poey, *Lepidopus* Gouan, *Benthodesmus* G. and B.

Fam. 97. **Trichiuridae.** Surface-fishes of the tropics. *Trichiurus* L. hairtails.

Fam. 98. **Xiphiidae.** Sword-fishes. The upper jaw is produced into a long sword-like weapon; pelagic fishes in all tropical and subtropical seas, very strong and swift, change much with growth, some can erect the dorsal fin above the water and use it as a sail; attain to 12 or 15 ft.; attack Cetaceans and vessels and can pierce thick planks; sword formed by prolongation of premaxillaries and maxillaries, with small villiform teeth on its lower surface, may be 3 ft. long and 3 in. across at base, flesh esteemed. *Histiophorus* C. et V. (*Istiophorus* Lac.), Ind. and Pac. with pelvics; *Tetrapturus* Raf., *Xiphias* L. sword-fish.

Fam. 99. **Carangidae.** Body more or less compressed oblong or elevated, with small scales or naked; teeth if present conical; dorsal spines few or slender or reduced; a more or less developed spine adnate to the soft portion of the anal, often preceded by a pair of spines separate from the rest of the fin; pelvics thoracic, sometimes small or absent; 10 abdominal and 14 caudal vertebrae. Inhabitants of tropical and temperate seas. First appear in cretaceous (*Platax*, *Vomer*, *Aipichthys*); extinct genera, *Pseudovomer*, *Amphistium*, *Archaeus*, *Ductor*, *Plionemus*, *Semiophorus*. Living genera are: *Caranx* Cuv., horse mackerels, *C. trachurus* Lac. the British horse mackerel; *Argyrosus* (*Selene*), *Micropteryx* (*Chloroscombrus*); *Seriola* Cuv., yellow tails; *Seriola*, *Seriolichthys*; *Naucratus* Cuv., *N. ductor* C. and V., pilot-fish, to 12 in., precedes and accompanies sharks and vessels; *Chorinemus*, *Lichia*, *Temnodon* C. and V. (*Pomatomus* Lac.), *T. saltator* L., skip-jack, trop. and sub-trop. seas; *Trachynotus*, *Pammelas* Gthr. (*Palinurichthys* Bleek), *Psettus*; *Platax* C. and V., sea-bats, Ind. Oc. and W. Pac.; *Anomalops*, deep sea; *Directmus*, *Equula*, *Gazza*, *Lactarius*, *Paropsis*, *Platystethus*, *Citula*, *Alectis*, *Hynniss*, *Vomer*. *Zanclus* C. and V., rocky islands of Pacific.

Fam. 100. **Coryphaenidae.** Large pelagic fishes of brilliant colours with *Coryphaena*, "dolphins," *Brama*, *Taractes*, *Pteraclis*, *Diana* Risso (*Luvarus* Raf.), *Ausonia*, *Mene*.

### Tribe 3. ZEORHOMBI.

Aberrant, strongly compressed Perciformes with very short pre-caudal region, culminating in asymmetrical forms and characterised by the combination of an increased number (6 to 8) of rays of pelvic fins with absence of hypural spine (by which the Berycidae are excluded), or by asymmetry of the skull in the forms in which the spine of the pelvic fin has been lost.

Fam. 101. **Zeidae.** No subocular shelf, premaxillae strongly protractile. Gill-membranes free from the isthmus, 7 to 8 branchiostegal rays; gills  $3\frac{1}{2}$ , pseudobranch well developed. Lower pharyngeal bones separate. Hypural bone large, without the basal knob or spine present in most Perciformes and in all Scombriformes. Dorsals and anals elongate, the former with a distinct spinous portion, the latter with 1 to 4 spines detached from the soft portion. Pelvics with 1 spine

and 6 to 8 soft rays. Scales small or minute. Air-bladder present. Marine fishes of temp. N. and S. hemispheres. Were it not for the  $3\frac{1}{2}$  gills this family might be regarded as the originator of the Pleuronectidae. *Zeus* Art., *Z. faber* L., john dory; *Cyttus*, *Grammicolepis*, *Cyttopsis*, *Zenion*, *Oreosoma*.

Fam. 102. **Pleuronectidae**. Flat-fishes. Cranium posteriorly normal, anteriorly with twisted vertex to allow 2 orbits on the same side, or one vertical and one lateral. The side on which the eyes are placed is generally the same in the same species, but it may vary. In the young fishes the two sides of the body are alike, and the eyes are one on each side, with normal cranium. The body is compressed laterally and high; it lies on the left or right side, the lower side being colourless. Gills 4, a slit behind 4th, with pseudobranch, without air-bladder. Abnormal specimens are found in which both sides are coloured (double flat-fishes); in such, the eye which shifts, frequently does so incompletely and remains on the top of the head; in some cases a notch is left on the anterior edge of the dorsal fin, suggesting the course along which the eye has moved. Caudal fin, if well developed, supported by a large hypural, generally without basal spine or knob. Dorsal and anal long, without spines. Pelvics usually with 5 to 7 soft rays. The eggs float. *Psettodes*; *Hippoglossus* Cuv., eyes on right side, dorsal fin commences above the upper eye, scales cycloid; *H. vulgaris* Flem., halibut, *Hippoglossoides* Gottsche, eyes right, dorsal fin commences above upper eye, scales ctenoid; *H. limandoides* Bl., rough dab. *Rhombus* Cuv., eyes left, dorsal fin commences on snout, *R. maximus* L., turbot, *R. laevis* Rond., brill. *Phrynorhombus* Gthr. (*Zeugopterus* Gottsche), eyes left, dorsal fin commences before the eye, scales ctenoid, *Ph. unimaculatus* Risso, top-knot. *Arnoglossus* Bleek, eyes left, dorsal fin commences on snout, *A. megastoma* Don., whiff, merry sole, *A. laterna* Walb., scald-fish; *Pseudorhombus*, *Rhomboidichthys*. Other genera with nearly symmetrical mouth, in which the dorsal fin commences on the snout, are *Citharus*, *Anticitharus*, *Brachypleura*, *Samaris*, *Psettichthys*, *Citharichthys*, *Hemirhombus*, *Paralichthys*, *Liopsetta*, *Lophonectes*, *Lepidopsetta*, *Thysanopsetta*. *Pleuronectes* Art., eyes right, dorsal commences above the eye, *Pl. platessa* L., plaice; *Pl. microcephalus* Donov., smear-dab, lemon sole of fishmongers, tasteless and wanting in firmness, occasionally passed off as the sole by unscrupulous cooks; *Pl. cynoglossus* L., craigfluke; *Pl. limanda* L., dab; *Pl. flesus* L., flounder; *Rhombosolea*. *Solea* Cuv., eyes right, dorsal fin commences before the eye, and is not confluent with caudal; *S. vulgaris* Quensel, common sole, the most esteemed of all food-fishes, young are called slips, nostril on the blind side not dilated; *S. lascaris* Risso (*aurantiaca* Gthr.), lemon-sole, one of the nostrils on the blind side dilated and fringed; *S. variegata* Donov., banded sole, thick-back; *S. minuta* Parn. (*lutea* Risso) little sole; *Pardachirus*, *Liachirus*, *Synaptura*, *Aesopia*, *Cynoglossus*, *Soleotalpa*, *Apionichthys* with imperfect eyes, *Ammopleuraps*, *Aphoristia* (*Symphurus*), *Plagusia*, *Achirus*, *Gymnachirus*.

#### Tribe 4. KURTIFORMES.

No bony stay for the preoperculum. With one dorsal fin only, much shorter than the anal, which is long and many-rayed. No suprabranchial organ. Scapula absent, the coracoid supporting 4 small somatids; pelvics thoracic.

Fam. 103. **Kurtidae**. Body compressed, deep in front, attenuated behind. Snout short. Villiform teeth on the jaws, palatine and vomer Indian and Pacific Oceans. One genus, *Kurtus*.

#### Tribe 5. **Gobiiformes**.

The sub-orbital ring is without a bony stay for the operculum. The gill-membrane attached to isthmus; gills 4, a slit behind the last; pseudobranch present. Pelvics inserted below pectorals with 1 spine and 4 or 5 soft rays; first dorsal of a few weak spines, sometimes absent; usually no air-bladder nor pyloric caeca. Carnivorous bottom fishes, some marine, others f. w.

Fam. 104. **Gobiidae**, as above. *Gobius* Art., the gobies, temp. and trop. coasts, 600 species, males of some species construct nests. Several British species. *Aphia* Risso (*Latrunculus* Gthr.), *A. pellucida*, laterally compressed, transparent fishes said to live only one year; *Crystallogobius* Gill, *C. Nilssonii*; *Euctenogobius*, *Lophiogobius*, *Doliichthys*, *Apocryptes*, *Evorthodus*, *Gobiodon*, *Triaenoporphichthys*. *Sicydium* C. and V., small f. w. fishes in rivulets of islands of trop. Indo-Pac.; *Lentipes*; *Periophthalmus* Schn., coasts of trop. Indo-Pac., leave the water at low tide and hop over the wet ground by means of their pectoral and pelvic fins and tail, the eyes are very movable and protrusible; *Boleophthalmus* very similar; *Eleotris*, *Trypauchen*; *Callionymus* L. dragonets, the mature males have the fin-rays produced into filaments *C. draco*, skulpin; *Mistichthys luzonensis* from the Philippines measures only half an inch, and is the smallest known vertebrate. *Vulsus*, *Benthophilus* from the Caspian, *Amblyopus*, *Orthostomus*, *Platyptera*, *Luciogobius*, *Oxymetopon*, and a large number of tentative Amer. and Asiatic genera.

#### Tribe 6. **Discocephali (Echeneiformes)**.

With characters of the family.

Fam. 105. **Echeneididae**: The Remoras. With a suctional transversely laminated oval disc on the upper surface of the head (the spinous dorsal fin modified), thoracic pelvics, with external spines; no air-bladder, no pseudobranch, no finlets; found in all seas; attach themselves to floating objects and other fishes. *Echeneis* Art.; *Phtheichthys*, *Remilegia*, *Remora*, *Rhombochirus*.

#### Tribe 7. **Scleroparei (Trigiliiformes)**.

Acanthopterygians with the pectoral girdle normal. The third sub-orbital bone extends across the cheek to or towards the preoperculum. This group—the mail-cheeked fishes—is a heterogeneous one, and subject to great variation.

Fam. 106. **Scorpaenidae**. Body oblong, more or less compressed; mouth large with villiform teeth, usually without canines; gills  $3\frac{1}{2}$  or 4, usually no slit behind the 4th gill; pelvics thoracic, of the percoid form with one spine and 5 soft rays; sometimes small; with air-bladder (usually) and large pseudobranchs; found in all seas as non-migratory fishes living about rocks; many with the skinny appendages resembling the fronds of seaweeds; many are viviparous. *Sebastes* C. and V., *S. norvegicus* C. and V.; *Sebastes* Gill, shores of the N.

Pac.; *Helicolenus*; *Scorpaena* Art., scorpion-fishes, no air-bladder; *Pontinus*, *Glyptauchen*, *Lioscorpius*, *Setarches*, *Pterois*, *Apistus*, *Agriopus*, *Synanceia*, the dorsal spines possess poison glands and inflict serious wounds; *Micropus*, *Chorismodactylus*, *Taenianotus*, *Centropogon*, *Pentaroche*, *Tetraroche*, *Prosopodasys*, *Aploactis*, *Trichopleura*, *Hemitripterus*, *Minous*, *Pelor*.

Fam. 107. **Heterolepidotidae (Hexagrammidae)**. Small shore fishes of the N. Pac.; the posterior nostril reduced to a minute pore. *Chirus* Steller, with several lateral lines; *Ophiodon* Gir., cultus cod, an important food fish on the Pacific coast of N. Amer.; *Agrammus*, *Pleurogrammus*, *Hexagrammos*, *Zaniolepis*, *Oxylebius*, *Anoplopoma* and *Erilepis* with normal nostrils.

Fam. 108. **Cottidae**. Body oblong or subcylindrical; teeth villiform in bands; gills  $3\frac{1}{2}$  to 4; 5th slit small or obsolete; body naked or variously armed with scales, prickles or bony plates; two dorsal fins (rarely one), the spinous being less developed than the soft and than the anal; pseudobranch present; air-bladder usually absent. Small fishes, mostly of rock pools and shores of northern regions, some found in f.w.; of no value as food. *Cottus* Art., bull-heads and miller's thumbs, small fishes from the shores and f.w.s. of N. temp. zone; *C. gobio* L., common miller's thumb, f.w.; *C. scorpius* and *C. bubalis*, etc., common Eur. marine species; *Cantridermichthys*, *Icelus*, *Platycephalus*, *Hoplichthys*, *Bembras*, *Bunocottus*, *Rhamphocottus*, *Triglops*, *Podabrus*, *Blepsias*, *Nautichthys*, *Scorpaenichthys*, *Hemilepidotus*, *Artedius*, *Ptyonotus*, *Polycaulus* *Jordania*, *Paricelinus*, *Alcidea*, *Chitonotus*, *Tarandichthys*, *Icelinus*, *Astrolytes*, *Archistes*, *Axyrias*, *Artedellus*, *Ruscarius*, *Rastrinus*, *Radulinus*, *Prionistius*, *Elanura*, *Melletes*, *Enophrys*, *Uranidea*, *Myoxocephalus*, *Megalocottus*, *Zesticelus*, *Gymnncanthus*, *Nautiscus*, *Ulca*, *Psychrolutes*.

Fam. 109. **Cyclopteridae (Discoboli)**. Lump-suckers. Short and thick with a smooth, tubercular or spiny skin; branchiostegals 6; gills  $3\frac{1}{2}$ ; 2 dorsal fins; pelvis thoracic, small, forming the bony centre of a sucking disc, by which they attach themselves to stones, etc.; air-bladder absent; northern seas. *Cyclopterus* Art., *C. lumpus* L. lump-sucker, cock-and-hen-paddle, skin with tubercles; *Eumicrotremus*, *Lethotremus*, *Liparops*; *Liparis* Art.; *L. vulgaris* Flem., sea-snail; *L. montagui* Cuv., diminutive lump-sucker; *Neoliparis*, *Bathyphasma*, *Careproctus*, *Gyrinichthys*, *Amitra*, *Paraliparis*, *Rhinoliparis*.

Fam. 110. **Agonidae**. Fishes of the cold seas, living among rocks or kelp; most of small size and fantastic form, not valuable as food; with 8 to 12 longitudinal rows of imbricated radially striated plates. *Percis* Scop. (*Hippocephalus* Swains.), *Agonomalus*, *Hypsagonus*, *Stelberina*, *Occa*, *Brachyopsis* (*Siphagonus*), *Pallasina*, *Leptogonus*, *Podothecus*, *Agonus* B. Schn., *A. cataphractus* L., sea poacher; *Stelgis*, *Agonopsis*, *Averruncus*, *Sarritor*, *Xystes*, *Bathygonus*, *Xenochirus*, *Odontopyxis*, *Bothragonus*, *Aspidophoroides*.

Fam. 111. **Triglidae**. Gurnards. Elongate, more or less fusiform, covered with scales or bony plates; gills 4, a large slit behind the 4th; pseudobranch and air-bladder present; latter said to have an open pneumatic duct (Günther); post-temporal forms an integral part of the cranium; pectoral large with broad base; 3 lower rays detached and used as feelers; all warm seas; grunt when taken out of water, caused either by escape of air through open pneumatic duct, or by compression of air



bladder by muscles. *Trigla* Art., Gurnards, with British species, *T. pini*, red gurnard; *T. lineata*, streaked gurnard; *T. hirundo*, sapphirine gurnard; *T. cuculus* Bloch's gurnard; *T. lyra*, the piper; *T. obscura*, the long-finned. *Prionotus* Lac., all but one American.

Fam. 112. **Peristediidae**. Deep-sea gurnards. *Peristedion* Lac. (*Peristethus* Kaup); *Vulsiculus*.

Fam. 113. **Cephalacanthidae**. Flying gurnards, with large pectorals, are able to move in the air, but for a shorter distance than the flying fish. *Cephalacanthus* Lac. (*Dactylopterus* Lac.).

#### Tribe 8. JUGULARES (BLENNIIFORMES).

Pelvises jugular; gill-openings in front of the pectoral fin, the base of which is vertical or subvertical.

Fam. 114. **Trachinidae**. Elongated, naked or covered with scales; teeth small; one or two dorsals; the spinous portion always shorter than the soft; the anal like the soft dorsal; no finlets; pelvises with 1 spine and 5 rays; carnivorous coast fishes of small size, world-wide, bottom fishes in small depths, except *Bathyraco*.

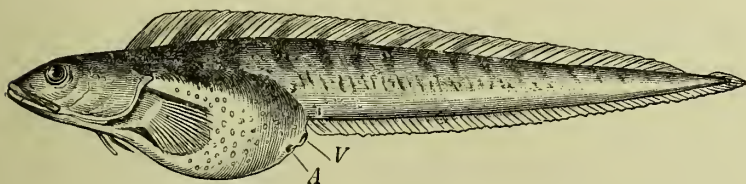


FIG. 128.—*Zoarces viviparus*. A anus; V urinogenital opening (from Claus).

**Uranoscopina**, Star-gazers. Eyes on upper surface of head *Uranoscopus*, *Leptoscopus*, *Agnus* (*Astroscopus*), *Kathcostoma*, *Anema*, *Dactyloscopus*, *Gillellus*, *Dactylagnus*, *Myxodagnus*.

**Trachinina**. Eyes more or less lateral. *Trachinus* Cuv., weevers; the mucus is poisonous, and they inflict poisonous wounds with their spines, they lurk in the sands, and are a caution to bathers. *T. draco* and *T. vipera* are British. *Champsodon*, *Bovichthys*, *Bathyraco*, *Chaenichthys*, *Aphritis*, *Acanthaphritis*, *Eleginus* C. and V., *Bembrops*, *Chimarrichthys*, *Cottoperca*, *Percophis*.

**Nototheniina**. Lateral line interrupted; dorsal fin of two portions, Antarctic. *Notothenia*, *Harpagifer*.

Fam. 115. **Trichonotidae**. *Trichonotus*, *Hemerocoetes*.

Fam. 116. **Gobiesocidae**. Suckers. Body rather elongate, tadpole-shaped, with smooth scaleless skin; breast with a broad sucking disc between the wide set pelvic fins; no spinous dorsal; no sub-orbital ring or air-bladder; gills  $3\frac{1}{2}$ ; marine fishes, living chiefly among loose stones between tide-marks. *Lepadogaster* Gouan; *L. gouanii* Lac.; *L. decandolii* Risso; *L. bimaculatus* Flem.; *Leptopterygius*, *Chorisochismus*, *Cotylis*, *Gobiesox*, *Diplocrepis*, *Crepidogaster*, *Trachelochismus*, *Caularchus*, *Brysetaeres*, *Rimicola*, *Arbaciola*.

Fam. 117. **Blenniidae**. Blennies. Lateral line various, often wanting, often duplicated; teeth various; pelvises jugular or sub-thoracic, with 1 spine and 1 to 3 soft rays, often absent; pseudobranch



present; gills 4, a slit behind the 4th; dorsal fin formed entirely of spines. Littoral fishes of great generic variety in all temp. and trop. seas; some in f.w., e.g., in the Italian Lakes. *Anarrhichas* Art., sea-wolf, to 6 ft., strong tubercular teeth, N. Seas; *A. lupus* L., wolf-fish (Fig. 117); *Anarrhichthys*; *Blennius* Art., littoral or attach themselves to floating objects, readily accustom themselves to f.w., some acclimatised in inland lakes (*B. vulgaris*). British species are: *B. gattorugine* Bloch., tompot; *B. ocellaris* L., butterfly blenny; *B. galerita* L.; *B. pholis* L., shanny; *Chasmodes*, *Petroscirtes* trop. Ind.-Pac.; *Salarias*, *Clinus*, *Cristiceps*, *Cremnobates*, *Tripterygium*, *Stichæus*; *Blenniops* Nils. (*Carelophus* Kröyer); *B. ascanii* Walb. British; *Centronotus* Bl. Schn. (*Pholis* Scop.); *C. gunellus* Bl. Schn., butter-fish, is British; *Apodichthys*, *Xiphidion*, *Cryptacanthodes*, *Pataecus*. *Zoarces* Cuv.; *Z. viviparus* L., a viviparous form in British seas (Fig. 128), *Blennophis*, *Nemophis*, *Plagiotremus*, *Neoclinus*, *Cebidichthys*, *Myxodes*, *Heterostichus*, *Dictyosoma*, *Lepidoblennius*, *Gunelichthys*, *Urocentrus*, *Stichæopsis*, *Sticharium*, *Notograptus*, *Pholidichthys*, *Pseudoblennius*, and a large number of other genera too numerous to mention.

Fam. 118. **Batrachidae**. With undivided post-temporal; gill-arches reduced to 3; gills 3, with slit behind last; no pseudobranch; head large, depressed; 2 dorsals; soft dorsal long; anal similar, but shorter; tail homocercal; carnivorous fishes of the warm seas; some ascending rivers. *Batrachus* Bl. Schn. (*Batrachoides* Lac.); *Thalassophryne* Gthr., two dorsal and opercular spines with poison sacs; *Porichthys*; *Opsanus* Raf. (*Batrachus* Jord. and Gilb.), toad-fishes, *O. tau* L.; *Daector*.

Fam. 119. **Ophidiidae**. Body more or less elongate; naked or scaly; median fins generally united, no separate anterior dorsal or anal; pelvics small or absent; tail tapering; without distinct caudal fin; gill-openings wide; gill-membranes not attached to isthmus. Marine fishes, except *Lucifuga*, partly littoral, partly bathybial.

**Brotulina**. Pelvic fins present, attached to the pectoral arch. *Brotula*, *Lucifuga*, subterranean waters of Cuba, eye reduced or absent; bathybial are *Bathynectes*, *Acanthonus*, *Typhlonus*, *Aphyonus*, *Rhinonus*; surface forms are *Brotulophis*, *Halidesmus*, *Dinematichthys*, *Bythites*; *Sirembo* and *Pteridium* are from moderate depths, and a considerable number of other genera (45 in all).

**Ophidiina**. Pelvic fins replaced by a pair of bifid filaments below the glossohyal. *Ophidium* Art.; *Op. barbatum* L.; *Genypterus*. *Lepophidium*, *Rissola*, *Chilara*, *Otophidium*.

**Congrogadina**. No pelvics, vent remoto from head. *Congrogadus*, *Haliophis*.

### Tribe 9. TAENIOSOMI (LOPHOTIFORMES).

Compressed, often ribbon-like fishes of doubtful affinities, probably related to the earlier Acanthopterygians, the pelvics when well developed having as many as 7 to 9 rays; dorsal fin extending from the head to the end of the tail; anal fin short or absent. Pectoral fin with 3 short somactids. Scales minute or absent. Deep-sea or pelagic fishes from the Atlantic, Mediterranean and Pacific.

Fam. 120. **Trachypteridae**. Ribbon-fishes. Deep-sea fishes often found floating dead on the surface with their tissues loosened by the

gaseous expansion. Body ribband-shaped ; dorsal fin as long as the body ; anal absent ; caudal feeble, or not in the longitudinal axis of the fish. In the young form some of the fin rays are enormously elongated. *Trachypterus* Gouan ; *Regalecus glesne*, king of the herrings ; *Stylophorus*.

Fam. 121. **Lophotidae.**

#### Sub-order 11. OPISTHOMI.

Air-bladder without open duct. Operculum well developed, hidden under the skin ; supraoccipital in contact with frontals ; pectoral arch suspended from the vertebral column far behind the skull ; no mesocoracoid ; pelvics absent ; median fins with spines.

Fam. 122. **Mastacembelidae.** F.w. fishes almost confined to the Indian and Ethiopian regions ; Acanthopterygian eels. They constitute part of the fish fauna of Lake Tanganyika. *Mastacembelus*.

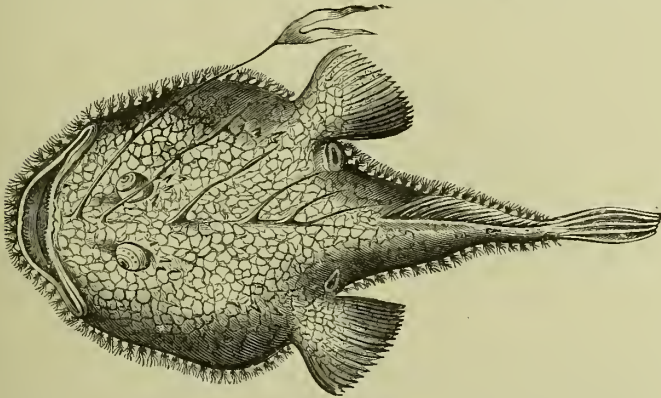


FIG. 129.—*Lophius piscatorius* (after Cuvier and Valenciennes, from Claus).

#### Sub-order 12. PEDICULATI (LOPHIIFORMES). Anglers.

Head and anterior part of body very large and without scales. The spinous dorsal fin is advanced forwards, composed of a few more or less isolated spines, often transformed into tentacles, or entirely absent ; pelvic fins, jugular with 4 or 5 soft rays, sometimes absent. Gill opening a small foramen in or near the axil, posterior to the base of the pectoral ; pseudobranch usually absent ; gills  $2\frac{1}{2}$ , 3, or  $3\frac{1}{2}$  ; air-bladder without duct. The somactids are elongated, forming a kind of arm which supports the broad pectoral fins and by means of which they are able to walk over moist ground, etc., in search of prey or to burrow in the sand or clasp foreign objects. Marine fishes chiefly of

the tropics and abysses. Bad swimmers; those found near the coasts lurk in the mud or sand or among stones or sea-weed, while the pelagic forms attach themselves to floating sea-weed.

Fam. 123. **Lophiidae.** *Lophius* Art., frog-fishes, anglers; *L. piscatorius* L. (Fig. 129), with above-mentioned names; also monk-fish, toad-fish, sea-devil; the anterior tentacle terminates in a lappet resembling a worm or piece of meat; is movable and is used as a bait; the terminal lappet can be rapidly regenerated; their spawn has the form of floating sheets of mucus, often of large size; remarkable for their voracity. *Ceratias*, *Himantolophus*, *Melanocetus*, *Oneiroides*, *Mancalias*, *Cryptosaras*, *Linophryne* are abyssal; *Antennarius* is pelagic; *Chaunax*, *Malthe* (*Ogcocephalus*), *Halieutaea*, *Dibranchus*, *Aegaeonichthys*, *Lophiomus*, *Pterophryne*.

### Sub-order 13. PLECTOGNATHI.

With rough scales or with ossifications of the cutis in the form

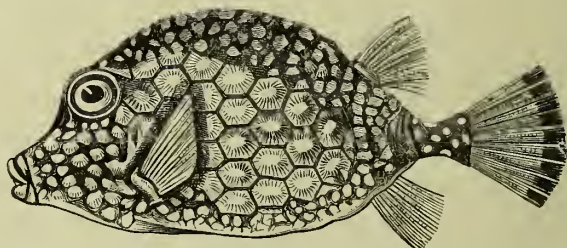


FIG. 130.—*Ostracion triquetrum* (Regné animal).

of scutes or spines; skin sometimes entirely naked. Skeleton incompletely ossified, with the vertebrae in small number. Gills pectinate, a narrow gill-opening in front of the pectoral fins. Mouth narrow; the bones of the upper jaw generally firmly united. A soft dorsal fin opposite to the anal; sometimes elements of spinous dorsal as well. Pelvics none or reduced to spines. Air-bladder without duct. Scapula suspended to cranium by a post-temporal. Inactive fishes, chiefly of the tropics.

#### Tribe 1. SCLERODERMI.

Supraclavicle vertical; somactids not enlarged, movably attached by ligament to the scapula and coracoid; all the vertebrae with a single neural spine; dentary and articular co-ossified.

Fam. 124. **Triacanthidae.** Covered with hard or spinous scales, teeth separate, with spinous dorsal, pelvics paired. Indian and W. Pacific Oceans. *Triacanthus*; *Triacanthodes*; *Halimochirurgus*, deep-sea.

Fam. 125. **Triodontidae**. Covered with small spiny bony laminae; teeth fused into a beak; without spinous dorsal and pelvics; abdomen with a dilatible sac; Indian Ocean. *Triodon*.

Fam. 126. **Balistidae**. Covered with juxtaposed movable scutes or with minute rough scales; teeth incisor-like; spinous dorsal with one to three spines; pelvics, if present, as short rough spine; flesh of many species poisonous. *Balistes* Art., file-fishes, trigger-fishes, trop. or sub-trop., feed on corals and molluscs, enemies of pearl-fisheries; to 3 ft.; *B. capricus* has been taken off Britain; *Monacanthus*, *Paraluteres*, *Pseudaluteres*, *Pseudomonacanthus*, *Alutera*, *Psilocephalus*.

Fam. 127. **Ostraciontidae**. Trunk-fishes. Encased in a carapace formed of large juxtaposed bony plates; teeth incisor-like; without spinous dorsal and pelvics. Tropical seas, living near bottom; about 20 species. *Ostracion* Art., coffer-fishes (Fig. 130); *Aracana*, *Lactophrys*.

## Tribe 2. GYMNOTONTES.

Supraclavicle oblique; lower three somactids enlarged and immovably united to the coraco-scapular cartilage, upper somactid small, suturally united to the scapula. Anterior vertebrae with bifid divergent spines; suture between dentary and articular visible; without spinous dorsal and pelvics; teeth fused to form beak; trop. and sub-trop. seas, a few in f.w.; when taken they frequently produce sound by expulsion of air from oesophagus; flesh usually poisonous.

Fam. 128. **Tetrodontidae**. Globe-fishes. Beak with median suture; skin naked or with movable spines; caudal fin present; can inflate the oesophagus with air and so distend the body; when dilated the spines of the scaleless skin become erected, and when in this condition they turn over and float at the surface belly upwards; in some cases the spines about the head can be erected by cutaneous muscles. *Tetrodon* L.; *T. lagocephalus* has been taken off Britain; *T. psittacus* (Brazil), *T. jahaka*, (Nile), and *T. fluviatilis* (E. Ind.) are in large rivers. *Ephippion*, *Tropidichthys*, *Xenopterus*, *Chonerinus*.

Fam. 129. **Diodontidae**. Porcupine-fishes. Beak without median suture, belly inflatable; trop. seas. *Diodon* Gthr.; *D. hystrix* L.; *Lyosphaera*.

Fam. 130. **Molidae**. Body compressed, very short, dorsal and anal fins confluent; no air-bladder, tail short, without caudal fin; beak without median suture; body non-inflatable; skin rough or tessellated; an accessory opercular gill; fishes of the open seas; apparently composed of a huge head to which small fins are attached; bask at the surface in calm weather; young very different in form to adult and described as a distinct genus, *Molacanthus*. *Orthogoriscus* Bloch, (*Mola* Cuv.); *O. mola* Bl. Schm., sun-fish, attains a large size; *Ranzania*.

## CHAPTER IX.

### DIPNOI.\*

*Scaly fish with gills and lungs, external and internal nares, cartilaginous autostylic-skull covered with osseous dermal scutes, persistent notochord with unsegmented sheath, and with an operculum covering the gill apertures. Paired fins with long segmented cartilaginous axes. Caudal fin diphyccercal or heterocercal. Branchiostegal rays absent. Heart with spirally twisted conus arteriosus. Palatal and mandibular teeth few, tuberculated, as though made up of fused denticles. The mid-brain roof is not divided into optic lobes.*

The important characters of the Dipnoi are the peculiar teeth, the acutely lobate often fringed paired fins, the autostylic skull, the internal opening of the nasal sac, the cartilaginous endoskeleton almost devoid of cartilage bone, the persistent uncontracted notochord and absence of vertebral bodies, the conus arteriosus, the incipient doubleness of the heart, and the presence of a vein resembling the inferior vena-cava. In consequence of the form of the skull, the vascular system and breathing arrangements, the possession of an internal as well as of an external opening of the nasal sac, the nature of the egg and the

\* Owen, *Lepidosiren*, *Trans. Lin. Soc.* 17, 1840. Hyrtl, *Lepidosiren paradoxa*, Prag, 1845. Günther, *Ceratodus*, *Phil. Trans.* 161, 1872. Huxley, *Ceratodus*, *Proc. Zool. Soc.*, 1876, p. 24. Bridge, *Skull of Lepidosiren*, *Trans. Zool. Soc.*, 14, 1897; p. 325. Fritsch, *Fauna der Gaskohle*, Bd. 2., 1888. Lankester, *Hearts of Ceratodus, Protopterus, etc.*, *Trans. Zool. Soc.* 10, 1879, p. 493. Boas, Herz u. Arterienbogen bei *Ceratodus* u. *Protopterus*, *Morph. Jahrb.*, 6, 1890, p. 321. W. N. Parker, *Anatomy of Protopterus*, *Trans. R. Irish Acad.*, 30, 1892, p. 109. Spence, *Blood-vessels of Ceratodus*, Macleay memorial volume, *Lin. Soc. N.S.W.*, 1893. Ehlers, *Zur Kenntniss der Eingeweide v. Lepidosiren*, *Nach. K. Gesellsch. d. W. zu Göttingen*, 1895. R. Burekhardt, *Das Centralnervensystem v. Protopterus annectens*, Berlin, 1892. Kerr, *External Features in the development of Lepidosiren*, *Phil. Trans.*, 192, 1900, p. 299. Semon, *Papers on Ceratodus by different authors in Zoologische Forschungsreisen in Australien etc.* Jena, 1898.



early development, the order has been said to be intermediate between the Fishes and Amphibia. By the form of the teeth and the autostylic character of the skull, they resemble the *Holocephali*; while in the structure of the paired fins, the scales, and, if we may judge by *Polypterus*, the form and function of the air bladder, they approach the Crossopterygian Ganoids. By their whole organisation they are essentially piscine, and in many features of their structure, e.g. the nature of their endoskeleton and the structure of their vertebral column they resemble the lowest fishes. In short they constitute an order of fishes which, while showing affinity to most of the other orders, are peculiar in possessing features which are not found in other fishes but which are found in *Amphibia*. This Amphibian tint, while not for one moment justifying an assignment of the order to the *Amphibia*, or even to an intermediate position between that class and *Pisces*, may by enlarging our conception of the range of piscine structure be of service to us in our speculative treatment of the numerous extinct forms which, always imperfectly preserved, are in many cases most difficult of interpretation.

The gill slits are covered by an opercular fold. There are no eyelids. The nasal sacs possess as in Teleosteans and Ganoids two openings, but one of these is into the mouth on each side of the vomerine teeth, the other on the under side of the head close to the mouth.

The tail is diphyccercal, and the pelvic fins are inserted a little in front of the anus. There are in *Ceratodus* two abdominal pores leading into the body cavity, one on each side of, but a little behind, the anus. In *Lepidosiren* abdominal pores are not found; in *Protopterus* it is said that there are two which join to open by a single pore just in front of the anus within the cloacal sphincter.

The scales lie in pockets of the dermis and resemble in structure the cycloid scales of Teleosteans. The superficial layer is without bone-cells, which however are found in the deeper fibrous layer. There is no ganoin.

In the vertebral column the notochord persists and is uncontracted, the sheath, which is invaded by cartilage, does not segment or ossify; there are dorsal and ventral arches which do not meet laterally on the notochordal sheath (except sometimes

at the hind end of the tail and in the first two or three segments), and intercalated pieces may occur. The ribs, arches, and fin-supports show a tendency to ossification.

The chondrocranium consists almost entirely of cartilage. In *Ceratodus* it is massive and completely developed, there being no fontanelles in the roof or floor. In *Lepidosiren* the trabeculae cranii have retained their primitive condition of rods of cartilage bounding a large pituitary fontanelle, and have not extended dorsally, so that the greater part of the side-walls and roof are formed of membrane bone. The notochord is continued into the base of the skull, with which the notochordal sheath of the vertebral column is continuously and immovably united. In *Lepidosiren* and *Protopterus* the first distinguishable neural arch is ossified and placed behind the foramen for the second spinal nerve, and the first rib (cranial rib) is articulated to the occipital cartilage. In *Ceratodus* it would appear that the number of neural arches which have been incorporated in the skull is greater. The two exoccipital bones are the only cartilage bones found in the chondrocranium.\* The space containing the membranous labyrinth is open to the cranial cavity as in Ganoids, Holocephali, and Teleosteans. The skull is completely covered dorsally (except over a part of the ethmoid cartilage) by dermal membrane bones, on the floor there is a parasphenoid and a trace of two vomers in the two chisel-shaped vomerine teeth in the front of the roof of the mouth. There are two large palatopterygoid bones, which meet in front beneath the ethmoid and carry two large, tuberculated, palatal teeth. Maxillae and premaxillae are absent. The suspensorium has the form of a triangular shelf, continuous with and projecting from the skull, and supported by the stout pterygo-palatine bone in front and by the squamosal behind. The quadrate region of this suspensorium is unossified. Meckel's cartilage is persistent and ensheathed by two, sometimes three, membrane bones, of which the splenials are of unusual size and carry the two large tuberculated teeth. The teeth consist of fenestrated bony tissue continuous with that of the jaws, and of dentine covered by enamel on the exposed tubercles. The hyoid is attached to the hinder upper part of the suspensorium where it passes into the auditory cartilage,

\* Fürbringer (*Anat. Anzeiger*, 24) finds that these do not belong to the chondrocranium, but are the neural arch of an incorporated vertebra.

and consists in *Ceratodus* of a small dorsal piece, identified by Huxley as the hyomandibular, and of a stout ossified ventral piece which joins its fellow of the opposite side. A post-temporal is present in *Protopterus* and *Ceratodus* but not in *Lepidosiren*. There are two opercular bones, the operculum and interoperculum, each of which carries on its inner side a small band of cartilage (cartilaginous opercular rays). The branchial arches are five in number, slender, and often unsegmented.

The pectoral girdle is placed just behind the head and consists of a cartilaginous coraco-scapular arch, continuous with its fellow ventrally. It is overlaid by a closely applied clavicle and supraclavicle (cleithrum). The skeleton of the pectoral fin is unibasal, rachistichous and mesorachic. It consists in *Ceratodus* (Fig. 138) of a segmented cartilaginous axis (axial somactids) which tapers distally and proximally is attached to a stout basal somactid. The latter is articulated to the shoulder girdle. Attached to the pieces of the axis are on each side a number of small segmented somactids which carry a fringe of dermatichia. The fin is therefore fringed on the crossopterygian type and its skeleton constitutes what has been called the "*archipterygium*." The pelvic girdle is a single piece of cartilage in the middle line, with a forwardly directed process. The pelvic fin skeleton is very similar to the pectoral. In *Lepidosiren* the paired fins are filamentous and the skeleton consists of the axis of *Ceratodus* only, without the lateral somactids and dermatichia. In *Protopterus* somactids and dermatichia are present, though in a reduced form.

**Gill-Clefts.** There is no spiracle; the hyoid arch bears a gill which in *Ceratodus* is a pseudobranch supplied by arterial blood, but in *Protopterus* is a gill supplied by a branch from the afferent vessel to the first branchial arch. In *Ceratodus* and *Protopterus* there are five gill-clefts, the last being behind the 4th branchial arch. In *Lepidosiren* the hyobranchial cleft is closed in the adult though open in the larvæ. The partitions between the gill-clefts are membranous septa to which the branchial lamellæ are attached, thus approximating to the condition found in Selachians. In *Ceratodus* the four anterior branchial arches bear a double row of lamellæ; in *Protopterus* and *Lepidosiren*\* the 1st and 2nd branchials are without gills,

\* There is considerable individual variation in the respiratory lamellæ of *Lepidosiren*.

the 3rd and 4th have a double series ; while in *Protopterus* the 5th arch bears one row of gills which are probably an extension of the hindermost row of the 4th branchial.

In *Protopterus* there may be three external gill-filaments just above the operculum. They are not present in all specimens. They are not found in the adults of the other two genera, though external gills are found in the larva of *Lepidosiren* (Fig. 134).

The stomach is a dilatation of the hind end of the oesophagus and the pylorus is at its hind end. The intestine is straight with a spiral valve, and is supported by a ventral as well as by a dorsal mesentery. The hind end of it is a cloaca and receives the urinary and generative ducts.

The spleen appears to be embedded in the wall of the stomach and there is a pancreas concealed round the bile duct and in the wall of the intestine. There are no pyloric caeca.

The lung of *Ceratodus* is single ; it lies on the dorsal side of the alimentary canal, but opens into the ventral wall of the oesophagus, round the right side of which it turns. It contains a central cavity communicating with air-cells in the thickness of its walls. The lungs of *Protopterus* and of *Lepidosiren* are very similar, but they are double except in front where they open into the oesophagus.

The heart shows a tendency to be divided into two lateral halves. This is most completely carried out in *Lepidosiren*, least so in *Ceratodus*. The conus arteriosus is well developed and twisted into a spiral (Fig. 131). It contains several longitudinal rows of valves ; most of these valves are small, but those of one row are enlarged (Fig. 131, B) and to a certain extent united so as to form a longitudinal valve which in the contraction of the heart divides the conus into two halves, in such a way that the venous blood is directed into the two posterior afferent branchial arteries of each side, while the arterial and the mixed blood is sent into the branchial arteries to the 1st and 2nd branchial arches. The ventral aorta is extremely short as in *Amphibia*, the branchial arteries arising close together immediately in front of the conus (Fig. 131 A).

In *Ceratodus* the sinus venosus is divided into a narrow left portion into which the pulmonary veins open and a larger right portion receiving the systemic veins (Fig. 131, *svp*, *sv*). Both of these open into the single auricle, which is partially divided by a septum arising from its dorsal wall (*w*).

This incomplete septum is continued into the ventricle. The conus presents traces of eight transverse rows of valves. The number in each row varies in different parts of the conus (posteriorly about eight, anteriorly four or even one). The valves of the first two rows and those of one longitudinal row are larger than the others. The longitudinal row referred to lies in the ventral middle line in the posterior part of the conus and to the right side in the anterior region (in consequence of the spiral twist which the anterior part of the conus has undergone). These valves are so enlarged and united with one another by fibres that they form the longitudinal valve above referred to.

In the heart of *Protopterus* the arrangements are very similar, except

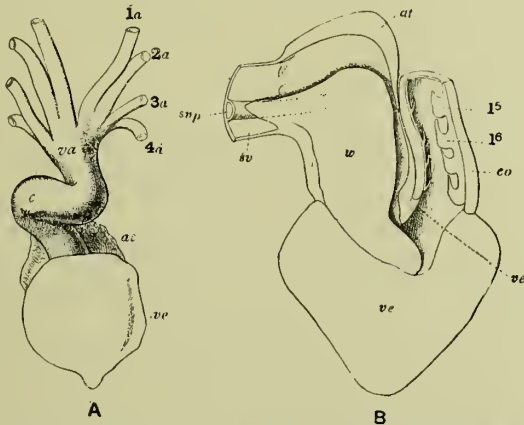


FIG 131. A. ventral view of heart of *Ceratodus* (after Boas). at, auricle; ve, ventricle; c, conus; 1a to 4a, arteries to the four branchial arches springing close together from the ventral aorta va.

B.—Median section through the contracted heart of *Ceratodus* slightly diagrammatic (after Boas); the posterior part of the conus only is shown. at, auricle; co, conus; ve, wall of ventricle; svp, left (pulmonary) division of sinus venosus; sv, larger right (systemic) division of sinus; w, imperfect auricular septum, the cavity of the auricle can be seen in the section passing on the ventral side of the free edge of this; 15, 16, the 5th and 6th valves of the row constituting the longitudinal fold.

that (1) the valves of the longitudinal row are more completely united to form the longitudinal fold; (2) there is in the anterior part a second longitudinal fold formed from two valves of the two first transverse rows; and (3) the other smaller valves of the conus are much less numerous than in *Ceratodus*.

In *Lepidosiren* the two longitudinal valves of the conus completely divide it into two parts, and the ventricular septum indicated in the other two genera is complete except for a small pore between it and the conus septum. The auricular septum is also well developed, though the meshes in the ventricular end of it may admit of some intercommunication through it.

The ventral aorta gives off three arteries on each side. The



posterior of these divides to form the afferent arteries to the 3rd and 4th branchial arches, on which a double row of gill-filaments are always present; it arises somewhat more dorsally than the two anterior vessels which go to the 1st and 2nd branchial arches, which are without gills in *Protopterus*. The anterior of these, viz. that to the first branchial arch sends a branch to the hyoid gill in *Protopterus*. The efferent vessels of each side unite to form one vessel (root of dorsal aorta), which joins its fellow to form the dorsal aorta. The carotid arteries pass off from the efferent vessel of the hyoid gill which joins the aortic root, and the pulmonary arteries arise from the roots of the aorta.

In *Ceratodus* the hyoid gill is a pseudobranch and is supplied by a vessel from the ventral end of the efferent vessel of the first branchial arch; its blood is returned into an artery called the anterior carotid, which goes to the head. The pulmonary artery also arises from the efferent vessel of the fourth branchial arch.

The anterior part of the venous system is constructed on the usual piscine type. In the posterior part there are some remarkable peculiarities which recall *Amphibia*. On the left side there is a posterior cardinal which arises in the left kidney and empties into the left ductus cuvieri; on the right side there is a vein which may be the right posterior cardinal, but which is called the inferior vena cava, which indeed it closely resembles; it arises in the right kidney, passes anteriorly through the liver, receives in *Protopterus* the hepatic veins, and opens directly into the sinus venosus. The kidney is supplied by the dorsal aorta and by the caudal vein.

In *Ceratodus* the hepatic veins fall into the sinus venosus, and there is an anterior abdominal vein formed by the union of a branch from each iliac vein (from the pelvic limb). It empties directly into the sinus venosus. Moreover in *Ceratodus* the left posterior cardinal and inferior vena cava are direct continuations of the two branches into which the caudal vein bifurcates; they receive from, but do not give blood to, the kidney. The venous blood to the kidney is partly derived from veins of the posterior body wall and partly from a branch of the iliac vein. In *Ceratodus* and possibly in all *Dipnoi* there is, as in *Elasmobranchii*, a sub-intestinal vein which lies along the spiral valve and joins the portal vein.

The **brain**\* presents the following features (Fig. 132). The

\* Burckhardt, *Das Centralnervensystem von Protopterus annectens*, Berlin 1892. Kerr, *Q.J.M.S.*, vol. 46, 1903, p. 428.

cerebrum is double and gives off the olfactory lobes from the dorsal surface anteriorly; each half contains a lateral ventricle, which is continued into the olfactory lobe. There is no thin pallium, but each lateral ventricle contains the usual choroid plexus which projects into it from its hind end, where its wall is continuous with the thin roof of the thalamencephalon (see below). Behind this the roof dips inwards as a fold, the *velum transversum*; then follows a protrusion of the roof with thin walls, behind which is the superior commissure, the attachment of the pineal stalk, and the posterior commissure. The pineal stalk is inclined forwards and ends in the pineal body which lies on this complex of structures. The roof of the mid-brain is not bilobed externally, and the cerebellum is small. On the dorsal side of the 4th ventricle, there is on each side a diverticulum of the membranous labyrinth called the saccus endolymphaticus, which gives off diverticula. The infundibulum presents lobi inferiores and a *sacculus vasculosus*.

Just in front of the *velum transversum* (Fig. 133) the roof of the brain is thin and folded, and swollen up. In *Lepidosiren* the velum is a paired structure, not extending across the middle line (Kerr).

The first spinal nerve is the hypoglossal; it perforates or notches the "exoccipital." The second spinal nerve either perforates the exoccipital (*Protopterus*) or emerges between the exoccipital and the first distinct neural arch.

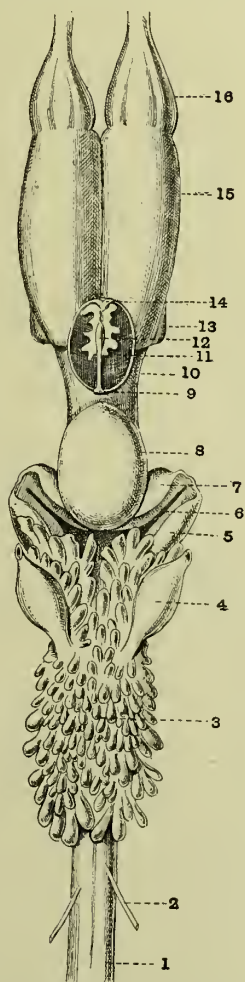


FIG. 132.—Dorsal view of the brain of *Protopterus* (after Burckhardt). 1 spinal cord; 2 dorsal root of first spinal nerve; 3 diverticula of 4 the saccus endolymphaticus; 5 medulla oblongata; 6 fourth ventricle; 7 cerebellum; 8 mesencephalon; 9 stalk of pineal body; 10 thalamencephalon; 11 velum transversum; 12 pineal body; 13 lobus hippocampi; 14 choroid plexus; 15 cerebrum; 16 olfactory lobe.

**Urinogenital Organs.** The kidneys\* are without nephrostomata in the adult; they are elongated glands not differentiated into meso- and meta-nephros. Each of them has a ureter which either joins its fellow before opening into the cloaca (*Ceratodus*) or the ureters open separately into a cloacal caecum derived in development from the fused hind ends of the longitudinal ducts. The larva possesses a pronephros on the Amphibian type with two funnels and an elongated glomerulus contained in an incompletely separated off portion of the body-cavity. The ovaries and testes are elongated bodies. The oviducts are convoluted tubes opening anteriorly and far forward into the body cavity and joining behind to open into the cloaca just in front of the ureters. The testis has a

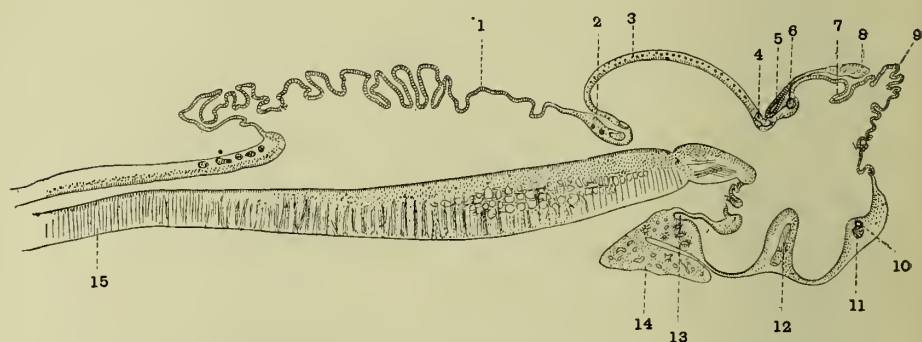


FIG. 133.—Longitudinal vertical section through the brain of *Protopterus* (after Burckhardt). 1 choroid plexus of 4th ventricle; 2 cerebellum; 3 mesencephalon; 4 posterior commissure; 5 pineal stalk; 6 superior commissure; 7 velum transversum; 8 pineal body; 9 choroid plexus; 10 corpus callosum; 11 anterior commissure; 12 optic chiasma; 13 sacculus vasculosus; 14 pituitary body; 15 spinal cord.

longitudinal duct extending along its whole course. This duct communicates with the tubuli seminiferi on the one hand and by a number of transverse tubes with the hinder part of the kidney. It ends blindly in front and behind, and has been fully made out in *Lepidosiren*; it probably exists in *Ceratodus*. A similar duct is described by Parker in *Protopterus*, where it is said to open into the cloaca and not to communicate by transverse tubes with the kidney. This is however denied by Kerr. The male possesses a well-marked vestige of the oviduct.

The egg is of considerable size and undergoes complete unequal cleavage. The early development is very like that of Amphibia

\* Kerr, *Proc. Zool. Soc.* 1901, p. 484.

and the blastopore persists as the anus. In *Ceratodus* the central nervous system arises by the closing in of a groove as in most vertebrates. In *Lepidosiren* the medullary canal has at first the form of a solid keel-like thickening of the ectoderm, as in *Lepidosteus* and Teleosteans. The young are hatched as larvae which possess external gills in *Lepidosiren*, but not in *Ceratodus*. Growth probably lasts for some time if not throughout life, and a length of three feet may be attained. It is quite probable that during this long period of growth the structure of the animal may change considerably, and that contradictory anatomical results may be explained in this way. It is probable that the fins can be regenerated.

In *Protopterus* there does not appear to be any marked external difference between the sexes, but in *Lepidosiren* the male

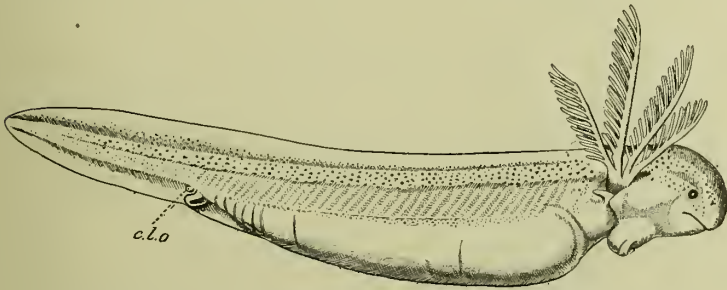


FIG. 134.—A larva of *Lepidosiren* 25 days after hatching, showing the external gills, the rudiments of the fore and hind limbs, and the cloacal aperture *c.l.o.* (after Kerr).<sub>1</sub>

acquires during the breeding season a large tuft of long highly vascular papillae on its pelvic fins. Both these genera breathe air when living in water, but the respiratory movements are less frequent than in the cocoon form.

*Ceratodus* is not a mud-fish. It never leaves the water. It is found in the dry season in the deep pools of the rivers in which it lives. These pools become very foul when the river shrinks in the hot season, and no doubt under these conditions the branchial respiration is largely supplemented by pulmonary.

*Lepidosiren* and *Protopterus* are true mud-fish. They bury themselves at the beginning of the dry season in the mud of the swamps in which they live. As the drying mud stiffens they retire deeper into the burrow, an opening always remaining at the upper end for respiration. In this burrow the *Protopterus*

lies with the body bent and the tail folded over the face, and surrounded by a cutaneous secretion of mucus containing earthy particles. The outer layer of this mucus which is in contact with the earth of the burrow hardens and constitutes the cocoon or capsule. The upper end of the capsule is closed by a kind of lid, on the surface of which is an aperture leading into a pipe of dried mucus which passes between the lips of the animal (Fig. 135). As the water diminishes the animal ceases its

branchial respiration and the lung respiration alone continues. *Lepidosiren* lies at the bottom of its burrow surrounded by mucus, but there does not appear to be a special cocoon with lid and pipe as in *Protopterus*.

Breeding takes place shortly after the return of the water and the liberation of the animal from the mud. This varies considerably in accordance with the season. *Lepidosiren* lays its eggs in underground burrows, which after descending vertically about one foot run horizontally for two to five feet. The male remains in the nest with the eggs in a curled up position.

All three genera take both vegetable and animal food.

The *Dipnoi* may be divided into two sub-orders or families. One of these—the *Sirenoidei*—includes the living genera and numerous fossil teeth, which are found only in the Jurassic and Triassic formations and on which the genus *Ceratodus* was originally founded. The bulk of the *Dipnoi* are, however, exclusively Palaeozoic forms. It is a noteworthy fact that the genus *Ceratodus* which existed in Triassic and Jurassic times has persisted to the present day, though no remains of it or of

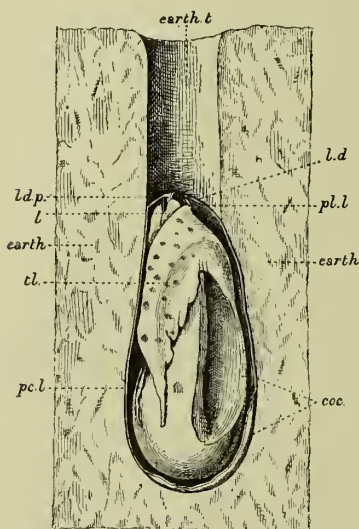


FIG. 135.—Diagram of the torpid *Protopterus* in situ (after W. N. Parker). The tube is open above, and the cocoon lies in the bottom of it. The pipe is shown leading into the mouth. coc cocoon; earth earthy mass round cocoon; earth. t burrow through earth; l.d. lid of cocoon; ld. p pipe from lid of cocoon; p.c.l pectoral fin; pl.l pelvic fin; t.l tail.



any other Dipnoan are found between the Jurassic and the present time.

The other sub-order includes Palaeozoic forms only. Some of these present, in the heterocercality of the tail and in the differentiation of the unpaired fin, features which are regarded by some anatomists as more primitive than the diphyrcercality and continuous unpaired fin of living forms. We however are not inclined to attribute so much importance to these facts of

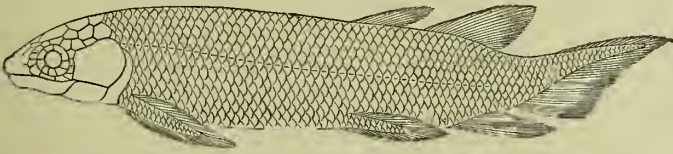


FIG. 136.—*Dipterus valenciennesii*. Ag. Old red sandstone,  $\frac{1}{2}$  nat. size, restored (from Woodward after Traquair).

structure. We think on the contrary that they show merely that there was considerable variability in the fins in the Palaeozoic forms and the particular combination of characters possessed by these organs in living Dipnoi is merely one which might quite well have been found—indeed is found—in the Palaeozoic Dipnoi.

1. **Ctenodipterini.** Skull with numerous small scutes, with jugular plates; vomerine teeth have not been observed. Devonian, Carboniferous, Permian. *Dipterus* Sedgwick and Murchison (Fig. 136). *Scaumenacia*, with heterocercal tails and two dorsal fins and an anal; *Phaneropleuron* Huxley, with diphyrcercal tail and distinct anal fin; *Ctenodus* Ag., *Sagenodus* Owen, *Uronemus* Ag., *Conchopoma* Kner, with diphyrcercal tail and continuous dorsal fin.

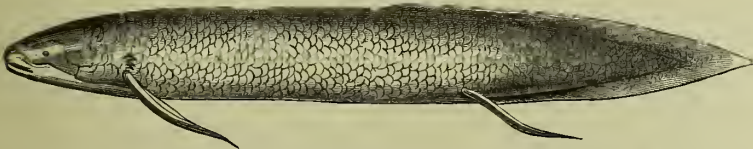


FIG. 137.—*Protopterus annectens* (from Claus).

2. **Sirenoidei.** Skull covered with few large scutes; with long, single dorsal fin and anal fin continuous with diphyrcercal tail-fin. Two vomerine teeth present. *Ceratodus* (*Epiceratodus*) Ag., with one lung, rivers of Queensland. Teeth of this or a closely allied genus are found in the Trias and Jurassic. The Dipnoan type is then lost until it appears in the three genera of the present day. *C. forsteri* Krefft, barramunda, rivers of Queensland. *Protopterus* Owen, with two lungs, swamps of tropical Africa. *Pr. annectens* Owen. *Lepidosiren* Fitz., with two lungs, trop. Amer. *L. paradoxa* Nat.

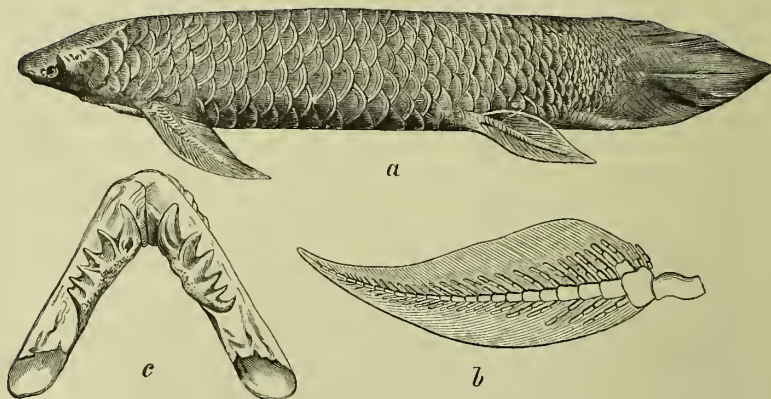


FIG. 138.—*a*, *Ceratodus forsteri*; *b*, its pectoral fin (after Günther). *c*, lower jaw with dental plates (after Krefft).

### Arthrodira.

The *Arthrodira* is a group of Devonian fishes showing some resemblance to and sometimes grouped with the *Dipnoi*. The vertebral column appears to have been unossified, but the dorsal and ventral arches and the fin-supports are weakly ossified. The head and anterior part of the body are covered with large bony plates; of which the head plates are movably articulated with the anterior body plates. The posterior part of the body appears to have been sometimes without armour, sometimes with large dorsal and ventral plates; the tail is heterocercal, without scales. They were probably autostylic; at any rate, no trace of a hyomandibular has been observed. The chondrocranium was probably unossified, but it is possible that in some genera there were exoccipitals and ossified parachordals. The pectoral girdle and fin have never been found, unless the slender hollow spines of *Brachydeirus* are related to them. Teeth are absent, or confined to the pterygo-palatine region, vomers, and lower jaw. Dorsal and anal fins are differentiated. These fishes are very unlike anything now living, and must have had a remarkable organisation. *Coccosteus* Ag., *Dinichthys* Newberry, including forms of very large size (head-shield sometimes a metre across), *Homosteus* Asmuss, *Brachydeirus* Koenen.

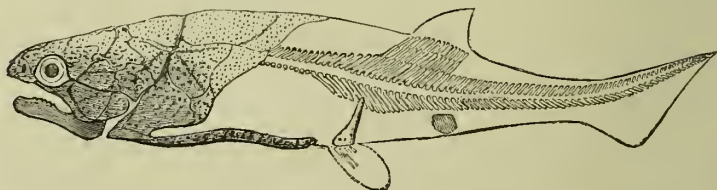


FIG. 139.—*Coccosteus decipiens*, restored,  $\frac{1}{2}$ , showing pelvic fins, the heterocercal caudal fin hypothetical (after Smith Woodward).

### Ostracodermi.\*

The fossils which are grouped together under this heading have been

\* Claypole, Pteraspidian fishes in the upper silurian rocks of N. America.

referred to various classes of animals, including *Crustacea* and *Arachnida*. They were first recognized as fishes by L. Agassiz, but their systematic position within that group is still quite uncertain, and it may well be that they are not fishes at all. They are confined to the upper Silurian and to the Devonian. Their internal skeleton is very little known. They are without any trace of jaws, visceral arches, paired fins and their girdles, and a segmented axial skeleton. The head and anterior part of the trunk are always invested by a powerful dermal armour, consisting of large plates, of which one covers the whole dorsal aspect of the head. The orbits are small and frequently placed near together on the dorsal surface of the cephalic shield as in *Limulus*. They are divided into three groups.



FIG. 140.—*Pteraspis rostrata*, restored,  $\frac{1}{2}$ , side view (from Smith Woodward).

**Heterostraci.** Head and anterior part of the body covered by a dorsal shield, rarely simple, usually composed of several pieces. The orbits are small and placed far apart on the outer edge of the dorsal shield. Hinder part of body covered by rhombic plates. The cephalic plates are without bone cells. *Pteraspis* Kner (Fig. 140), dorsal shield narrow in front and prolonged into a rostrum, with a median spine behind; *Palaeaspis* Claypole, *Cyathaspis* Lank.

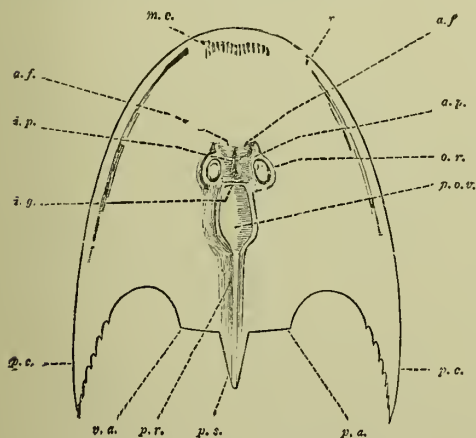


FIG. 141.—Cephalic shield of *Cephalaspis Agassizi* (after Lankester, from Woodward),  $\times \frac{1}{2}$ , L. Old Red Sandstone. *af*, antorbital fossae; *ap* antorbital prominences; *ig* interorbital ridge; *mc*, marginal cells; *or* orbital rim; *pa* posterior angle; *pc* posterior cornu; *pov* postorbital depression; *pr* posterior ridge; *ps*, posterior spine; *r* rim.

**2. Osteostraci.** Head covered by a large dorsal shield on which the two orbits lie near together (Fig. 141) and which contains bone cells; body covered with rhombic scales. *Cephalaspis* Ag. (Fig. 141), the posterolateral angles of the shield are produced and there is a median spine, dorsal and anal fins with well-developed rays, upper Silurian and Devonian. *Tremataspis* Schmidt, upper Silurian.

**3. Antiarcha.** Head and body covered by an armour of symmetrically arranged bony plates. Orbits close

*Quart. J. of Geol. Soc.*, 1857, 13, p. 48. Huxley, *Cephalaspis and Pteraspis*, *Ibid.*, 12, 1856, p. 100; 1858, 14, p. 267; 1861, 17, p. 163. Lankester and Powrie, *Cephalaspidae*, *Palaeont. Soc.*, 1868.

together on the dorsal surface of the head. Head and lateral plates with grooves for the sensory canals. An appendage, covered with plates and supposed to be the pectoral fin, is attached on each side in front. A short dorsal fin, with fulera in front. Tail covered with scales. Devonian. *Pterichthys* Ag. (Fig. 142), *Asterolepis* Eichw., *Bothriolepis* Eichw.

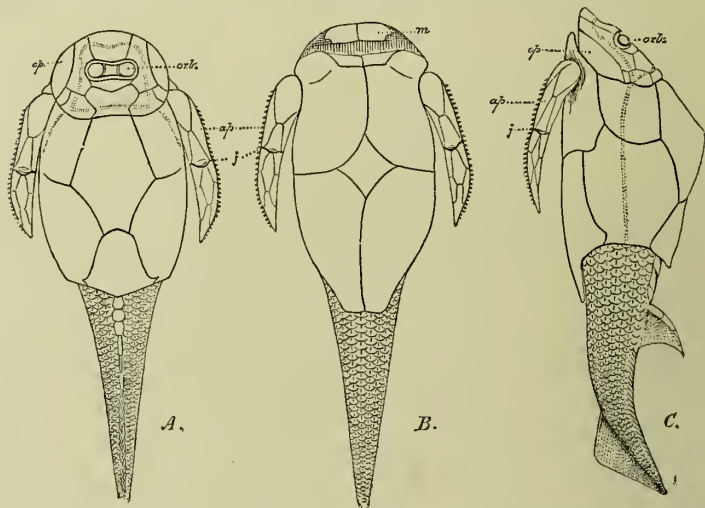


FIG. 142.—*Pterichthys milleri*, restored after Traquair  $\times \frac{1}{2}$ . *ap* lateral appendages (? pectoral); *j* joint in appendage; *m* supposed upper jaw with notches for narial opening; *op* operculum; *orb* orbits; double dotted lines indicate grooves for sensory canals.

**Ichthyodorulites.** Fin spines consisting of dentin or vasodentin and probably Selachian are indicated by this term. Some of them have been assigned to genera of which nothing is known but these spines. They are found in Palaeozoic rocks. Of such genera may be mentioned *Ctenacanthus* Ag., *Onchus* Ag., *Homacanthus* Ag., *Psammosteus* Ag.

**Conodonts** are minute denticles met with from the Lower Silurian to the Carboniferous Limestone; they are sometimes compared with the teeth of lampreys. They consist of a single cusp or of a series of cusps on one base, and appear to be formed of structureless concentric lamellae. They might be teeth of Molluscs or Annelids.



## CHAPTER X.

### CLASS AMPHIBIA.\*

*Cold-blooded Vertebrata with naked scaleless skin (except in Gymnophiona), with pulmonary and usually with transitory or permanent branchial respiration, with two occipital condyles and without amnion or allantois. The limbs when present are on the pentadactyle type and the heart is provided with two auricles, one ventricle and a conus arteriosus.*

The *Amphibia* stand in an intermediate position between fishes and reptiles. Whereas in the general form of their body and in certain anatomical features they are more reptilian, in the young state they are markedly piscine and in their full-grown condition they exhibit many important piscine characters.

They differ from fishes and resemble the higher *Vertebrata* in five important respects: (1) they are without fin-rays (dermotrichia), (2) they possess a limb constructed on the pentadactyle type, (3) the periotic capsule possesses a fenestra ovalis and a stapes, (4) paired posterior cardinal veins are absent in the adult, (5) a cloacal bladder is present. On the other hand they present the following features in which they resemble fishes and differ from the higher forms: (1) the presence of functional

\* Lacépède, "*Histoire naturelle des quadrupèdes ovipares et des serpents*," Paris, 1788-9. Merrem, "*Beiträge zur Geschichte der Amphibien*," 3 vols. Leipzig, 1790-1821. Daudin, "*Histoire Générale et particulière des Reptiles*," 8 vols, Paris, 1802-1803. J. G. Schneider, "*Historia amphibiorum naturalis et litteraria*," Jena, 1799-1801. J. Wagner, "*Natürliches System der Amphibien*," Stuttgart, 1828-33. Duméril et Bibron, "*Erpétologie générale*," 9 vols. Paris, 1834-55. E. Schreiber, "*Herpetologica europaea*," Braunschweig, 1875. G. A. Boulenger, "*Catalogue of the Batrachia Gradientia and Salientia in the British Museum*," 2 vols, London, 1882. H. Gadow, "*Amphibia and Reptiles*," Cambridge Natural History, London, 1901. A. Davison. A contribution on the anatomy etc. of Amphiuma means, *Journal of Morphology*, xi, 1985. Ecker's *Anatomie des Frosches*, 2nd Ed. by E. Gaupp, 1897.



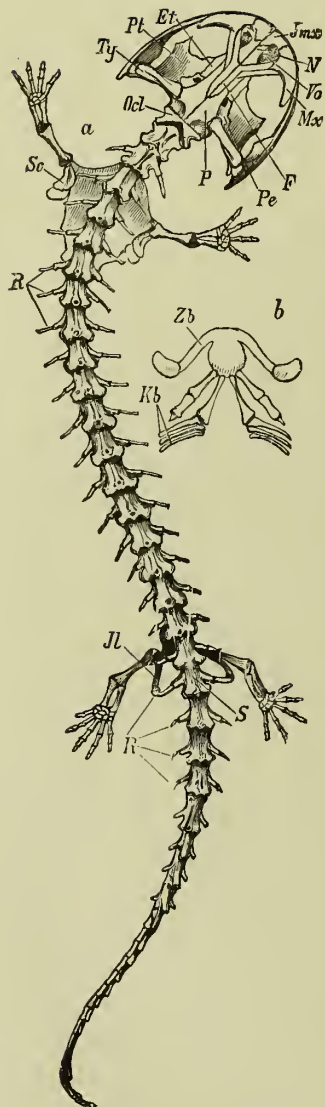


FIG. 142.—Skeleton of *Menopoma alleghaniensis* (from Claus). *Et* orbitosphenoid; *F* frontal; *Jl* pelvic girdle; *Jmx* premaxilla; *Mx* maxilla; *N* nasal; *Ocl* exoccipital; *P* parietal; *Pe* prootic; *Pt* pterygoid; *R* ribs; *S* sacral vertebra; *Sc* scapula; *Ty* squamosal; *Vo* vomer. *h* Hyoid apparatus; *Zb* hyoid; *Kb* branchial arches.

gill-slits and gills, (2) a single artery—the ventral aorta—alone leaves the heart, (3) there are only ten pairs of cranial nerves, (4) the presence of a functional pronephros in the larva, (5) the sexual part of the kidney is distinct from the testis and not incorporated into it as an epididymis, (6) the character of the ovum and the early development, (7) the absence of an amnion and allantois, (8) the presence of functional lateral line sense-organs.

On the whole it will be generally admitted that they stand nearer to fishes than they do to the higher forms, and that Huxley's inclusion of them with *Pisces* in a group which he called *Ichthyopsida* has a solid basis of fact. Nevertheless it must not be forgotten that the higher *Amphibia* present certain subtle features of approach to the Reptiles which are not shared by the lower members of the group. We refer especially to the asymmetry of the systemic aortic arches in the *Anura* (p. 284), and to the apparent abortion of the sexual part of the kidney in the male *Alytes* (p. 293).

In the main the *Amphibia* are aquatic in their habits: the majority live in or near water, and in almost all the congress of the sexes takes place and the eggs are laid in water. But

burrowing (*Gymnophiona*), arboreal (tree frogs) and purely terrestrial forms are found.

The vertebral column consists of separate, ossified vertebrae, which vary in number from over 250 in large specimens of some *Gymnophiona*, a variable but considerable number in the *Urodela* (Fig. 142), to nine in the *Anura*.\* The first vertebra, sometimes called the cervical, has two concave surfaces for articulation with the paired occipital condyles. In the *Urodela* it has a forwardly directed process of its centrum which has been identified as the odontoid process; in this case it must be regarded as the axis vertebra, the atlas having fused with the skull. It is without ribs and usually without transverse processes. The remaining vertebrae may be divided into trunk vertebrae, one sacral vertebra (two in *Pelobates*, *Pipa*, *Hymenochirus*, absent in *Siren* and *Proteus*) and, except in *Anura*, caudal vertebrae. Most or all the trunk vertebrae carry short ribs (Fig. 143, *R*) which are two-headed in *Gymnophiona* and most Urodeles. The sacral vertebra is without ribs in the *Anura*, but has them in the *Urodela*. In the *Anura*, in which there are almost always eight presacral vertebrae, the sacral vertebra is followed by an unsegmented bony rod, the *os coccygis* or urostyle, which is without spinal cord or any trace of notochord in the adult. Indications of segmentation may sometimes be discerned in the front end of this (Fig. 143, *Pte*). The caudal vertebrae of the *Urodela* are provided with complete haemal arches enclosing the tail blood vessels. The vertebrae are amphicoelous in the *Gymnophiona* and lower *Urodela*, the notochord being persistent

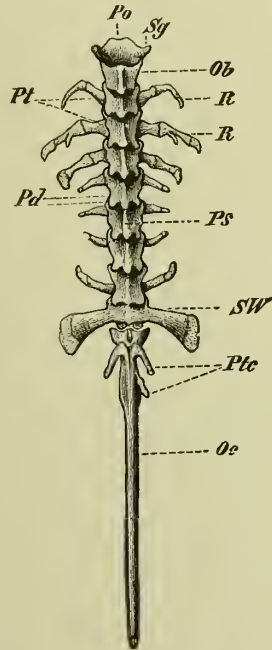


FIG. 143.—Vertebral column of *Discoglossus pictus* (after Wiedersheim). *Ob* neural arch; *Oe* urostyle; *Pd* zygapophysis; *Po* supposed odontoid process; *Ps* neural spine; *Pt* transverse process; *Pte* transverse processes of caudal vertebrae (urostylar); *R* ribs; *Sg* articular concavities for occipital condyles; *SW* sacral vertebra.

\* *Hymenochirus* has only seven vertebrae.

and continuous. In the higher *Urodela* (most *Salamandridae*) the vertebrae are opisthocoelous. In the *Anura* they are usually procoelous, though occasionally opisthocoelous and the notochord is for the most part obliterated.

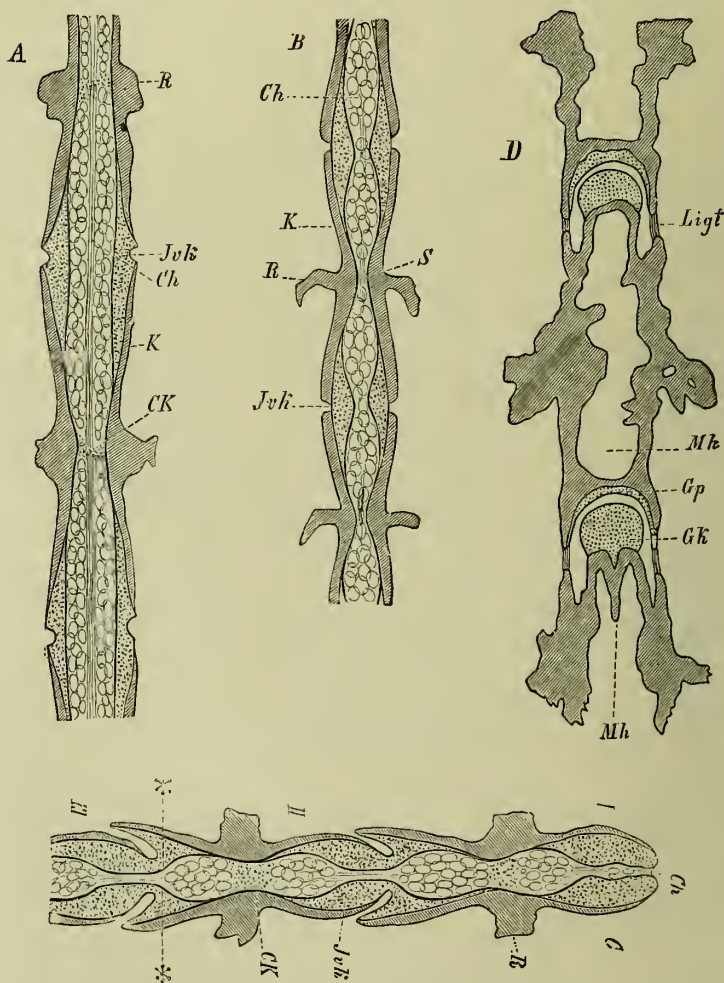


FIG. 144.—Longitudinal sections through the vertebral columns of some Urodels (after Wiedersheim). A *Ranidens*, B *Amblystoma*, C *Spelerpes*, D *Salamandrina*. I, II, III, the three anterior vertebrae; *Ch* notochord; *CK* intra-articular cartilage; *Gp*, *Gk* articulating cup and ball; *Jvk* intervertebral cartilage; *K* bone of centrum; *Lig* intervertebral ligament; *Mh* marrow cavity; *R* transverse process; *S* vertebral constriction of the notochord; \*\* the intervertebral cartilage.

In the lower *Urodela* the notochord is constricted first vertebally, but later owing to the great development of the unossified intervertebral connecting cartilage (Fig. 144, *A* and *B*, *Jvk*) it also becomes encroached upon intervertebrally. This great development of intervertebral cartilage is the marked feature of the amphibian vertebra. In some forms (Fig. 144 *C*) the intervertebral encroachment is very considerable, so great indeed that in most Salamandrines the notochord is entirely suppressed and the intervertebral cartilage is segmented into a cup and ball joint, one part uniting with the centrum of the anterior and the other with that of the posterior vertebra (Fig. 144 *D*). The bony tissue of the vertebral body would appear to make its appearance, in some cases at least, before the perichordal tissue has developed into cartilage. In the centre of the vertebral bodies of certain forms some cartilaginous tissue appears (Fig. 144 *A* and *C*, *CK*), which is doubtless derived from the perichordal cartilage, though it has been supposed by some anatomists to be notochordal and therefore hypoblastic in origin.\* In the *Anura* the notochord persists in a few forms vertebally throughout life (*Rana*).

The skull † of the Amphibia presents the following characteristics. The cartilage is largely persistent, there being but few cartilage bones; the occipital region rarely has more than the two exoccipitals which furnish the two occipital condyles; basioccipital, supraoccipital, basisphenoid, alisphenoid and presphenoid bones are always or almost always absent; there is no interorbital septum; well-developed paired frontal, parietal and nasal membrane bones are found in the roof and an unpaired parasphenoid and paired vomers in the floor; the jaw suspension is autostylic, the palato-quadrate bar being united at each end with the skull; the auditory region presents, for the first time, a *fenestra ovalis* which is filled up by a cartilaginous plate, the *stapes* (see p. 276). The quadrate, which in some cases remains cartilaginous, is covered by a membrane bone, the squamosal (paraquadrate). The visceral arches are in the larva five in number (hyoid and four branchial). These become variously reduced in the adult according to the condition of the breathing organs, but the hyoid and traces at least of two branchials generally persist together with a median ventral copula, of which

\* For a fuller account of the morphology of the vertebral column and ribs of Amphibia see F. M. Balfour, *Comparative Embryology* vol. 2, London, 1885. H. Gadow, *Phil. Trans.* 1896, vol. 187, p. 1-57. E. Göppert *Morph. Jahrb.*, 22, 1895.

† In addition to the textbooks already cited (Reynolds, Marshall, etc.) see Stöhr, *Z. f. w. Z.*, 33 and 36 for the development of the skull; Gaup, *Primordial cranium etc. of Rana fusca*, *Morph. Arbeiten*, 2; and W. K. Parker's various memoirs in the *Phil. Trans.* of 1871 (Frog), 1877 (Urodeles), 1881 (Batrachia); A. Davison *op. cit.*



they are processes. The hyoid is attached dorsally, directly or by ligament, to the auditory capsule or to the quadrate.

In the *Urodela* the cartilaginous cranium is much reduced. Cartilage is found in the roof and floor of the skull in the occipital region only. In front the trabeculae remain separate both dorsally and ventrally, so that there are large supracranial and basicranial fontanelles filled in by the overlying membrane bones (parietals, frontals, and parasphenoid). In some of the lower forms (*Proteus*, *Necturus*) the trabeculae retain throughout life the form of narrow cartilaginous bars. The auditory capsules possess a prootic and one or more other periotic bones, and in the anterior

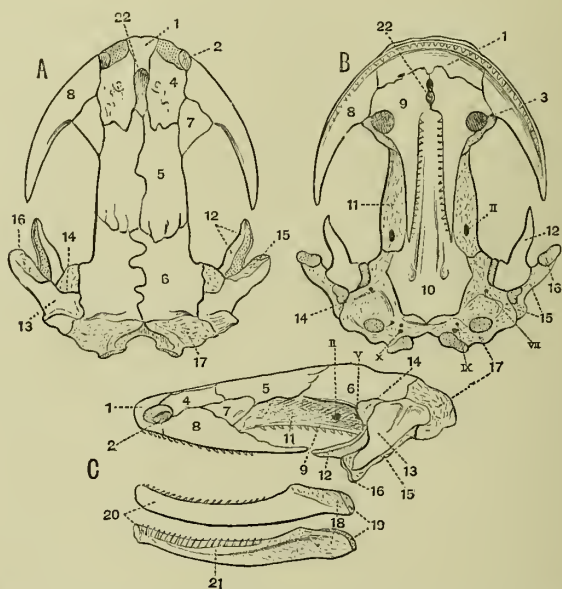


FIG. 145.—A dorsal, B ventral, C side view of the skull of the newt (*Triton cristatus*)  $\times 2\frac{1}{2}$  (after Parker, from Reynolds). The cartilage is dotted, the cartilage bones are marked with dots and dashes, the membrane bones are white. 1 premaxilla; 2 anterior nares; 3 internal nares; 4 nasal; 5 frontal; 6 parietal; 7 prefronto-lacrymal; 8 maxilla; 9 vomero-palatine; 10 parasphenoid; 11 orbitosphenoid; 12 pterygoid; 13 squamosal; 14 prootic region of exoccipito-periotic bone; 15 quadrate; 16 quadrate cartilage; 17 exoccipital region of exoccipito-periotic; 18 articular; 19 articular cartilage; 20 dentary; 21 splenial; 22 middle narial passage; II, V, VII, IX, X, foramina for exit of corresponding cranial nerves.

part of the sphenoid region there is a cartilage bone, the orbitosphenoid (Fig. 145, 11). The ethmoid region (nasal capsules) is unossified. The parietals and frontals are separate bones and the parasphenoid is not dagger-shaped. The vomer is double and usually fused with the palatine (Fig. 145, 9). There is a prefrontal in front of the orbit, with which a lacrymal element is supposed to be fused (?). There is a palato-ptyergoid bar in the larva, but in the adult the pterygoid and palatine bones are usually not connected. The quadrato-jugal is represented by ligament only. In the lower forms the quadrate is directed forwards as in the larva of all Amphibia, but in the higher forms it stands out at right angles or



may even be inclined backwards. The lower jaw presents articular, dentary, and splenial elements. Teeth may be present on the premaxillae, maxillae, vomeropalatines, and parasphenoid, and on the lower jaw. The visceral arches are generally reduced to the hyoid and two branchials in the adult, but sometimes four (*Siren*, *Amphiuma*, etc.) or three (*Necturus*, *Proteus*) pairs of branchials persist in the adult (Fig. 145 bis, A). There is no tympanic cavity in Urodeles.

In the *Anura* (Fig. 146) the cartilage of the cranium is much more developed, there being a complete cartilaginous floor and roof, which latter however contains some fontanelles. The two orbitosphenoids are replaced by a single "girdle" bone which extends into the hinder part of the ethmoid region and is called the sphenethmoid (*Et*). The parietal and frontal (*Fp*) are fused and the parasphenoid is dagger-shaped (*Ps*). The suspensorium slopes backwards and the palatopterygoid arch persists as a bar extending from the ethmoid to the suspensorium. Quadrato-jugals (*J*) are present, reaching from the maxilla to the quadrate. The lower jaw contains a mento-meckelian cartilage bone at the symphysis (ossified mento - meckelian cartilage of the larva). A tympanic cavity, communicating with the pharynx by a eustachian tube is present, and the stapedial plate is connected by a cartilaginous, partly ossified, rod, the columella auris, with the tympanic membrane, which is supported by a cartilaginous ring. Teeth are found on the premaxillae, maxillae, vomers, and the lower jaw, though the latter is frequently edentulous. The visceral arches (Fig. 145 bis, B) of the adult are represented by a large basilingual plate in the floor of the mouth which is connected with the otic region of the skull by the curved hyoid arches. All the four branchial arches and part of the copula of the larva completely disappear, the processes (including the bony thyrohyals) on the basilingual plate of the adult being new formations.\*

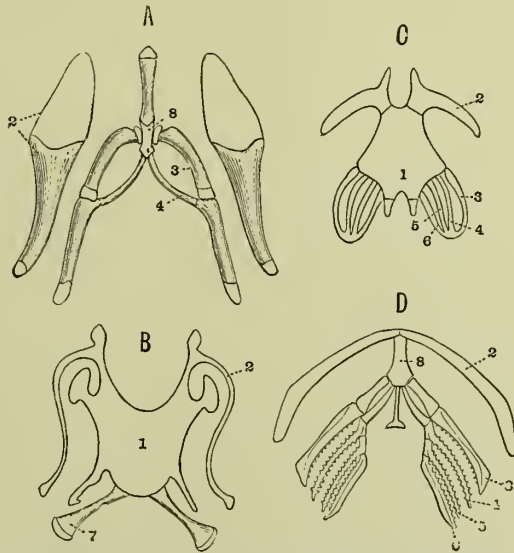


FIG. 145 bis.—Visceral arches of, A *Triton cristatus*; B *Rana temporaria*; C tadpole of *Rana*; D *Siredon pisciformis* (from Reynolds). The bone is shaded and the cartilage left white. 1, basilingual plate; 2, hyoid arch; 3, first, 4, second, 5, third, 6, fourth branchial arch; 7, thyrohyal; 8, copula.

As has already been stated, short two-headed ribs are often

\* Ridewood *P. Z. S.*, 1897, p. 577.

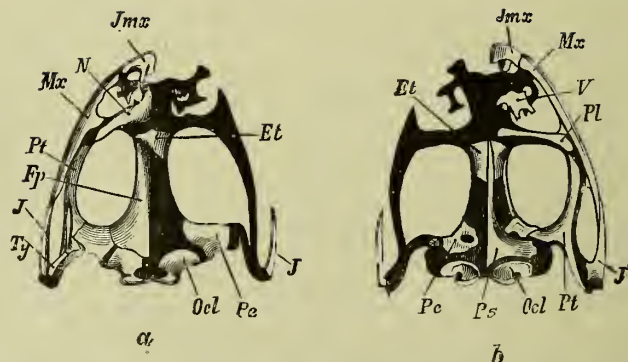


FIG. 146.—Skull of *Rana esculenta* (from Claus). *a* dorsal, *b* ventral view. The membrane bones of one side are removed. The cartilage is shaded dark. *Et* girdle-bone (sphenethmoid); *Fp* frontoparietal; *J* quadrato-jugal; *Jmx* premaxilla; *Mx* maxilla; *Nx* nasal; *Ocl* exoccipital; *Pc* prootic; *Pl* palatine; *Ps* parasphenoid (right half cut away); *Pt* pterygoid; *Ty* squamosal (paraquadrates); *V* vomer.

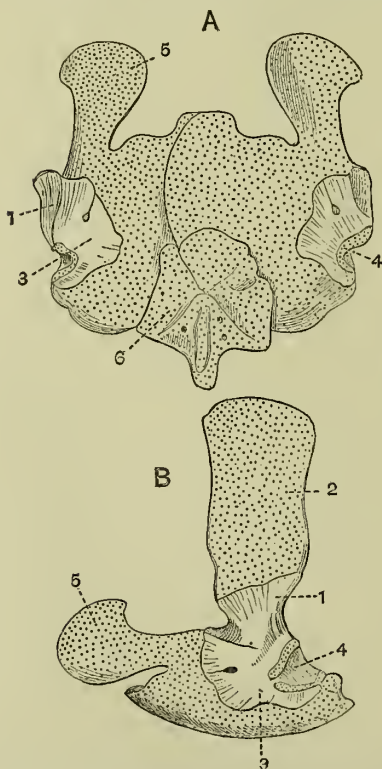


FIG. 147.—A, ventral, B, lateral view of the shoulder girdle and sternum of *Triton cristatus* (from Reynolds, after Parker). 1 scapula; 2 suprascapula; 3 coracoid; 4 glenoid cavity; 5 precoracoid 6 sternum.

present on many of the trunk vertebrae of the Urodeles. In the *Anura* they are generally absent, but in a few forms (e.g. *Discoglossus*, *Xenopus*) they are present on the anterior vertebrae. In no Amphibian do the ribs reach the sternum.

The sternum in the Urodeles is a cartilaginous plate lying behind and interposed between the coracoids (Fig. 147, *C*). In *Anura* the sternum lies partly in front of and partly behind the ventral union of the coracoids (Fig. 148). The part in front is called the *omosternum* (episternum, presternum), the part behind is the sternum proper, which expands behind into the cartilaginous xiphisternum (*13*).

In the *Urodela* the pectoral girdle is mainly cartilaginous being ossified only in the neighbourhood of the glenoid cavity (Fig. 147). The coracoids overlap one another ventrally and are articulated with the anterior end of the sternum. They are without a fenestra, but possess a well marked precoracoid. There is no clavicle. The radius and ulna are separate and there are usually four and never more than four digits in the manus (3 or 4 in *Siren*, 3 in *Proteus*, 2 or 3 in *Amphiuma*), the pollex probably being absent. The carpus is cartilaginous in the lower and ossified in the higher Urodeles. When four digits are present, it typically consists of a proximal row of three

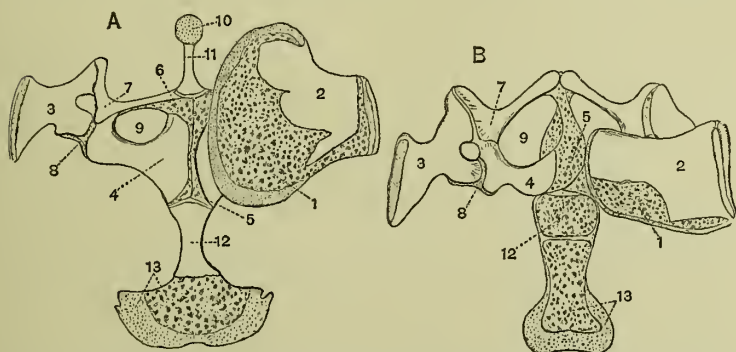


FIG. 148.—Pectoral girdle and sternum of A, an old male frog (firmisternal), B, an adult female *Docidophryne gigantea* (arciferous). From Reynolds. In both, the left supra scapula is removed. The unshaded parts are ossified; the parts marked with small dots are hyaline cartilage, those with large dots calcified cartilage. 1, calcified cartilage of suprascapula; 2, ossified part of same; 3, scapula; 4, coracoid; 5, epicoracoid; 6, precoracoid; 7, clavicle; 8, glenoid cavity; 9, coracoid fenestra; 10, 11, episternum (omosternum); 12, sternum; 13, xiphisternum.

pieces, a distal row of four, and a centrale; but there is often a certain amount of fusion and suppression of the carpalia and sometimes there is more than one centrale (*Megalobatrachus*).

In the *Anura* (Fig. 148) the scapular portion of the pectoral girdle is divided into an incompletely ossified suprascapula and an ossified scapula, and the coracoid portion possesses a fenestra dividing it into a cartilaginous, usually slender, precoracoid and a stouter ossified postcoracoid (often called coracoid). The epicoracoid (cartilaginous) is the ventral portion of the coracoid which meets (firmisternal) or overlaps (arciferous, Fig. 148 B) its fellow in the middle line. In the fore-limb the radius and ulna are fused, the carpus is usually reduced, and there are four

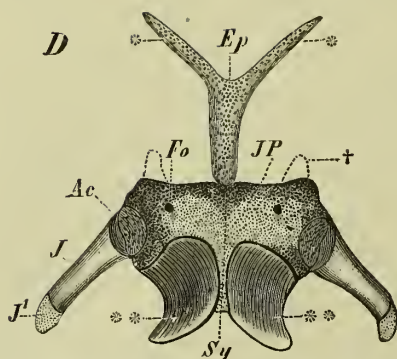


FIG. 149.—Ventral view of pelvic girdle of *Salamandra* (after Wiedersheim). *Ac* acetabulum; *Ep* epipubis; *Fo* foramen for obturator nerve; *J*, *J'* ilium; *JP* pubis; *Sy* symphysis; \*\* ischium.

complete digits and a much reduced pollex which is represented only by a short metacarpal.

In the *Urodela* the ilium of the pelvic girdle (Fig. 149) is vertically directed and the ischio-pubis is a flat plate which meets its fellow; the ilium and the ischial part of the ischio-pubis are ossified. There is often an epipubis, developed independently of the pubis and corresponding to the pre-

sternum of the pectoral girdle. The tibia and fibula are not fused and there are usually five digits. The tarsal elements are often complete, but there may be some fusion and more than one centrale.

In the *Anura* the ilium (Fig. 150) is elongated and directed backwards and the ischiopubis is fused with its fellow to form a disc. The ilium and ischium are ossified, but the pubic portion consists of cartilage which may become calcified. In *Xenopus* there is a small epipubis. The tibia and fibula are fused and there are usually five digits with trace of a prehallux. The tibiale and fibulare (intermedium absent) are much elongated and partially fused and the distal tarsals are reduced.

The **skin** of the Amphibia is usually soft and moist owing to the secretion of cutaneous glands. In the young larva it is ciliated. In some forms it is covered with warts, and in toads it is dry. Epidermal scales and except in the *Gymnophiona* dermal scales are never present in living forms. In the extinct *Stegoce-*

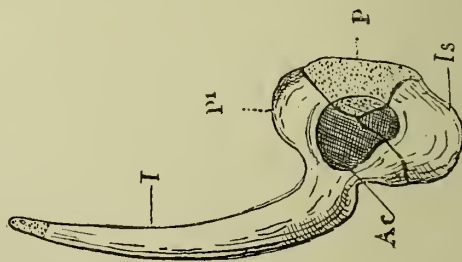


FIG. 150.—Side view of pelvic girdle of *Rana esculenta* (after Wiedersheim). *Ac* acetabulum; *I*, *P*<sup>1</sup> ilium; *P* pubis; *Is* ischium.

*phali* there is a well developed dermal skeleton, and in some *Anura* bony plates, which are sometimes united to the subjacent vertebrae, are present beneath the dorsal integument (*Ceratophrys*, etc.).

Horny thickenings of the epidermis are sometimes found on the ends of the digits giving rise to claws (e.g. *Onychodactylus*, *Xenopus*), and in other places (e.g. on cutaneous excrescences, hand of male frog, etc.). In all Amphibians the stratum corneum periodically peels off and the animal is said to cast its skin.

**Lateral line** sense-organs are present in the larvae and in aquatic forms on the head and in longitudinal rows (usually three) on the body (Fig. 151). The latter are innervated by the lateral line branch of the vagus. The skin is almost always pigmented and the colours are often brilliant. The pigment is

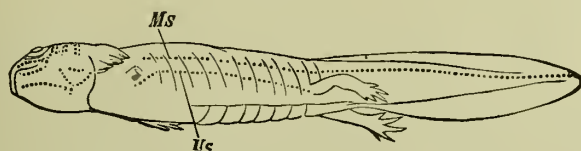


FIG. 151.—Larva of *Salamandra maculata* (after Malbranc from Claus).  $\frac{1}{2}$  Ms, Us rows lateral line sense-pits.

found in the epidermis (brown or yellow), and in branched cells in the cutis, where it may be black, brown, yellow or red. Colour change \* is a widespread phenomenon in Amphibians and is under the control, though not necessarily the voluntary control, of the nervous system. The secretion † of the cutaneous glands is very generally poisonous, especially in those with bright yellow markings, e.g. *Salamandra maculosa*, *Bombinator*, *Dendrobates*.

The lateral **muscles** are divided into myomeres after the piscine manner in the lower Urodeles, but in the higher forms this segmentation is lost.

The **brain** ‡ is small and distinguished by the small size of the cerebellum. The cerebral hemispheres are separate and

\* Biedermann, W., *Pflüger's Arch. Physiologie*, 51, p. 455.

† Boulenger, in *Natural Science*, 1, 1892. *Par&toids* are aggregations of cutaneous glands forming swellings on the sides of the head of some forms.

‡ Burchhardt, R., "Hirn. u. Geruchsorgan von *Triton* u. *Ichthyophis*," *Z. f. w. Z.*, 152, 1891, p. 369.



contain lateral ventricles. In the *Anura* the olfactory lobes are united across the middle line, in the *Urodela* they are separate. The pineal body is disconnected from its stalk and lies outside the skull in *Anura*. There does not appear to be any parietal organ or pineal eye.

There are ten pairs \* of cranial nerves arranged very similarly to those of fishes, excepting that in the abbranchiate forms the sense-organ branches (ophthalmicus superficialis, mandibularis externus, buccalis of the 7th, and lateral line branch of the vagus) have disappeared.

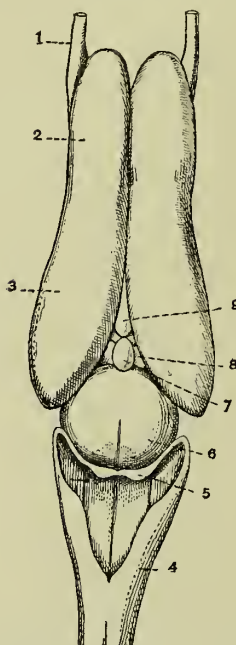


FIG. 152.—Dorsal view of the brain of *Triton cristatus* (after Burekhardt). 1, olfactory nerve; 2, olfactory lobe; 3, cerebral hemisphere; 4, medulla oblongata; 5, cerebellum; 6, optic lobes; 7, pineal body; 8, thalamencephalon; 9, choroid plexus.

They pass out of the skull by the foramen jugulare and unite into a single ganglion, the *ganglion jugulare*, from which pass out the glossopharyngeal and the vagus. The glossopharyngeal immediately dilates into a ganglion. It is a mixed nerve, supplying the anterior slip of the petrosal muscle and the mucous membrane of the pharynx and tongue, and, as stated above, it is connected by an anastomosing branch with the hyomandibular of the seventh. The vagus usually leaves the ganglion jugulare in two

\* von Plessen u. Rabinovicz, *Die Kopfnerven v. Salamandra maculata im vorgerickten Embryonalstadium*, München, 1891. Strong, The cranial nerves of Amphibia, *Journal Morphology*, 10, 1895, p. 101.

branches, the auricular and the main stem. The auricular is a sensory nerve to the skin. The main stem is a mixed nerve which contains the elements of the spinal accessory or 11th nerve of higher types (branch to the *m. cucullaris*). Its motor fibres supply the three posterior slips of the petrohyoid muscle, the laryngeal muscles and one of the shoulder-girdle muscles (interscapularis). There are no occipital and spino-occipital nerves (ventral vagus roots) in *Amphibia*.

In the *Anura* (Fig. 153) there are only ten pairs of spinal nerves and the spinal cord is shorter than the vertebral column, ending in the filum terminale (Fig. 153). In the *Urodela* the spinal nerves are more numerous and the spinal cord extends along the caudal region. In adult *Urodeles* \* and aglossal *Anura* the first spinal nerve is without a dorsal root; in the phaneroglossal *Anura* it is absent in the adult and the first spinal nerve, which leaves the spinal canal between the first and second vertebrae, is really the second. This second spinal nerve joins the brachial plexus but it

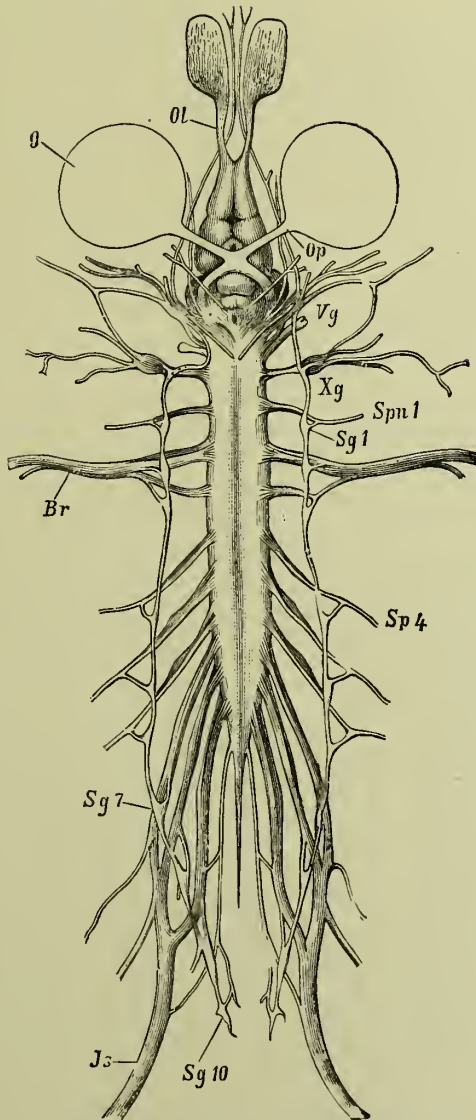


FIG. 153.—Nervous system of the frog (after Ecker). *Br*, brachial nerve; *Js*, ischial nerve; *O*, eye; *Ol*, olfactory nerves; *Op*, optic nerve; *Spn 1*, first spinal nerve; *Sg 1-10*, the ten ganglia of the sympathetic system; *Vg*, gasserian ganglion; *Xg*, ganglion of vagus.

\* This nerve is present with both roots in the embryo, but the dorsal root disappears in development. It resembles in this respect the occipito-spinal nerves of fishes.

gives off a strong branch to the tongue which constitutes the *hypoglossal*. In the frog the ganglion of the posterior root extends on to the common stem, and the dorsal and ventral rami of the spinal nerves both arise from it.

The **sympathetic** is distinct and connected with the ventral rami of the spinal nerves by rami communicantes. In the Urodeles it extends along the whole length of the body into the caudal canal. In the *Anura* it commences anteriorly in the skull as a cord leaving the ganglion prooticum, receives a branch from the ganglion jugulare, and dilates in the neck into the first ganglion of the sympathetic chain, which is connected by a ramus communicans with the first (second) spinal nerve (Fig. 153). This is followed by nine ganglia, each of which is connected with its spinal nerve by one, or in the case of the posterior ganglia by more than one, ramus communicans. The tenth ganglion is small and not always distinguishable.\*

**Sense organs.** The nasal sacs are always provided with internal nares. The eyes are reduced and covered by the skin in the subterranean and cave-forms (*Gymnophiona*, *Proteus*, *Pipa*). Eyelids, both upper and lower, are present in the *Salamandridae*, but absent in other Urodeles. In the *Anura* there is an upper eyelid and a movable nictitating membrane which is sometimes called the lower eyelid. In *Bufo* there is in addition a small lower lid. In the *Anura* there is a retractor bulbi muscle by means of which the large bulb of the eye can be drawn back. Lacrymal glands are absent, but there is an Harderian gland in the inner angle of the orbit of the *Anura* which opens within the nictitating membrane. There is a fenestra ovalis (vestibuli) in all *Amphibia*, and in many *Anura* a fenestra rotunda (cochleae) as well. There are three semi-circular canals, and a small cochlea was discovered by Deiters in the frog, and is probably present in other *Amphibia*.\* The tympanic cavity and membrane are absent in *Gymnophiona* and *Urodela*, and in some *Anura* they are much reduced or even absent (*Pelobatidae*, *Bombinator*, *Phrynisus*, *Batrachophrynus*, etc.). In most *Anura* they are present, though the membrana tympani is not always visible on the exterior. In the *Aglossa* the eustachian tubes join and have a single opening into the pharynx; in other forms they remain separate. The columella auris extends from the fenestra ovalis to the tympanic membrane. It lies outside the tympanic cavity, but projects into it. Its internal end, called the stapes or operculum, fits into and fills the fenestra ovalis; its outer end is connected with the membrana tympani. In the *Aglossa* the outer end expands into a cartila-

\* See *Corrigenda*

ginous plate which is coextensive with the membrana tympani. The shaft of the columella is frequently ossified, its two ends remaining cartilaginous. In the *Urodela*, in which it exists embedded in the muscles, its stapedial portion may be ossified and it is connected to the quadrate by ligament. It is probably homologous with the hyomandibular of fishes, though in the *Amphibia* it is never connected with the hyoid arch. The membrana tympani is attached to a cartilaginous ring.

The cup-like sense organs of the lateral line found in the aquatic forms and in the larvae of land forms have already been referred to (p. 273).

**Alimentary canal.** The mouth opening is a wide slit. Teeth, which are ankylosed to the bones, are present upon the premaxillae, maxillae, and vomers, sometimes on the dentaries, palatines, and parasphenoid. They are absent in *Pipa* and some toads. The tongue is immovable in *Urodeles*, absent in *Aglossa*, movable and free behind in other *Anura*, in which it is used as a prehensile organ. The posterior nares and eustachian tubes have already been referred to. Salivary glands are not present. In many male *Anura* the lining of the buccal cavity is produced into sacs, the *vocal sacs*, which act as resonators. In *Rhinoderma* they are used as nurseries for the young. Oesophagus, stomach, small intestine and rectum are present. The hind end of the rectum is called the cloaca and possesses a median ventral appendage, the bladder.\* The urinary and generative ducts open into the cloaca. The cloaca opens to the exterior by the anus. Liver and pancreas are present, and the former has a gall bladder.

The **thyroid**, unpaired in its origin, but becoming paired later, is present; and an organ representing the **thymus** and derived as epithelial buds from some of the branchial pouches is present close to the angle of the lower jaw (in the *Anura* behind the tympanic cavity and beneath the depressor mandibulae muscle).

The **body-cavity** is completely divided into the pericardial and peritoneal cavities. The peritoneal cavity extends forwards on each side of the pericardial. Abdominal pores are absent.

\* So-called allantoic bladder, though the *Amphibia* have no allantois in the embryo.



Nephrostomes are very generally present and will be dealt with under the urinogenital organs.

**Respiratory organs.** The skin is an important organ of respiration in all *Amphibia*, and in some abranchiate Urodeles it is the sole\* respiratory organ, lungs being entirely absent (*Desmognathinae*, *Plethodontinae*, *Amblystoma opacum*, *Salamandra perspicillata*). In such forms there is no pulmonary vein and the auricular septum is perforated by a large aperture. In all other members of the group lungs are present, and in some of the Urodeles gills and gill-slits as well. With very few exceptions the larvae are provided with gills. It is this combination of branchial and pulmonary respiration which is found in the adults of some forms and at some period in the life-history of nearly all, which confers a special interest on the breathing and vascular mechanisms† of the *Amphibia* and necessitates their being treated at some length.

With a few exceptions (for which see the systematic part and p. 296), all *Amphibia* are hatched as larvae, and possess while in that condition gill-slits and external gills. In all cases which have been fully investigated the rudiments of six visceral arches and of five pharyngeal pouches (Fig. 154) are laid down in development: the arches are the mandibular, the hyoid, and four branchial; the pouches are the mandibulo-hyoid, the hyobranchial, and the pouches between the successive branchial arches, there being no pouch behind the fourth branchial arch. Of these pouches the first (Fig. 154, *HM*) rarely‡ acquires an external opening; in the frog it gradually fades away and the tympanic cavity is formed later in its neighbourhood. The others (Fig. 154) become perforate and give rise to the four gill-clefts, which are found in the larvae of *Urodela* and *Anura*. The external gills, which are formed before the gill-clefts become perforate, are three in number on each side; they are branched structures and are attached to the dorsal ends of the three anterior branchial arches. These are the only gills found in

\* It has been suggested that the lining of portions of the alimentary canal may cooperate, *vide* Wilder, *Anat. Anzeiger*, 9, 1894, p. 216 and 12, 1896, p. 182; Lönnberg, *Zool. Anzeiger*, 19, 1896, p. 33.

† Boas J. E. V., *Morph. Jahrb.*, 7, 1882, p. 488; and 13, p. 115. Maurer F., *Ibid.*, 14, 1888, p. 175.

‡ It appears to do so in the Coecilian *Hypogeophis* and a small dorsally placed cleft (spiracle) is formed, but it is doubtful if this cleft becomes perforate in any other Amphibians.



the *Urodela* ; but in the *Anura* in which the gill-openings become covered by a membranous operculum (fold of skin growing back from the hyoid arch), the external gills atrophy and are replaced

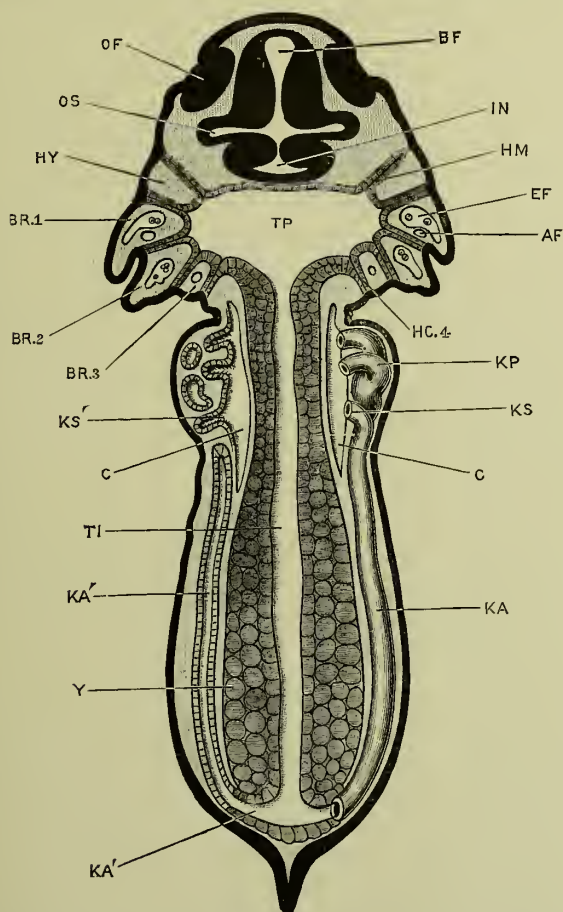


FIG. 154. — Horizontal section of the head of a tadpole at the time of hatching  $\times 40$  (after Marshall). *AF* afferent vessel of first branchial arch; *BF* fore brain; *BR1* first, *BR2* second, *BR3* third branchial arch; *C* body-cavity; *EF* efferent vessel of first branchial arch; *HM* hyomandibular pouch; *HY* hyoid arch; *IN* infundibulum; *KA* archinephric duct of right side, *KA'* of left side; *KP* pronephros; *KS* third opening of right pronephros, *KS'* ditto of left pronephros; *OF* olfactory pit; *OS* optic stalk; *TP* pharynx; *TI* intestinal region of enteron; *Y* yolk cells.

by a series of very similar but smaller structures developed along the more ventral portions of all four branchial arches. These are the internal gills, so called from their position beneath the operculum and not from any essential difference between

them and the external gills. Like the latter they are branched cutaneous structures covered by ectoderm. There is a double row of these gills on each of the first three branchial arches and one row on the fourth. In all the *Anura* and in most of the *Urodela* the gill-clefts close and the gills atrophy when the adult state is reached, but in a few of the *Urodela*, the so-called Perennibranchiates (*Proteus*, *Necturus*, *Siren*, etc.), some of them persist throughout life (for details, see systematic part). In the *Amphiumidae* the gills disappear but the last cleft usually persists, and in the genus *Amblystoma* the animal sometimes becomes sexually mature in the larval condition and does not metamorphose (*Siredon*, the axolotl). This phenomenon of the retention of larval characters in the sexually mature state has been called *neoteny*, or *paedogenesis*; it is not confined to *Amblystoma* but is found occasionally in the genus *Triton* (*Molge*). An analogous phenomenon is presented by many tadpoles and by some Urodeles, in which the metamorphosis is occasionally considerably retarded, but the larvae do not acquire sexual organs.

Gill-rakers, analogous to the gill-rakers of fishes, are found on the branchial arches of many forms. They consist of processes containing a peculiar form of connective tissue. In the larva of the salamander and in the tadpole of the frog there is one row of them on the first and fourth arch and two on the second and third. In the tadpole they are especially well developed and form a filtering apparatus which detains even the smallest particle.

In the *Urodela* the gills are not covered by an operculum, but a slight cutaneous fold from the hyoid arch represents this structure. All *Amphibia* with the exception of the lungless forms referred to on p. 278 possess lungs. These are simple sacs with more or less sacculated walls; in the *Anura* they open either directly or by short bronchi (*Aglossa*) into a laryngo-tracheal chamber which communicates by the slit-like glottis with the pharynx. The laryngo-tracheal chamber is supported by cartilages which can be identified with some of those found in the larynx of the higher forms, and in the *Anura* contains vocal chords. In the *Gymnophiona* and some of the more elongated Urodeles (*Siren*, *Amphiuma*, *Cryptobranchus*) there is a median tracheal tube supported by cartilages. Respiration is effected by a swallowing movement, the air being drawn into the mouth through the nares with the mouth closed. The

*Urodela* can only make a slight noise, but the *Anura* have a considerable voice, which is much intensified by the vocal sacs of the mouth and larynx.

**Vascular system.** There is always a special anterior section of the ventricle, the *conus arteriosus*, which is rhythmically contractile and guarded by semilunar valves at its two ends. Moreover there is a further resemblance to fishes in the fact that the ventricle (conus division of it) gives off only one artery, the ventral aorta or truncus arteriosus. It is true that this vessel is always very short and that in the *Anura* it is actually divided into two by a horizontal septum, but its homology with the ventral aorta of fishes and embryos cannot be disputed. In possessing this structure the *Amphibia* present a piscine feature, and one in which they markedly differ from the Reptilia and higher Vertebrata. In other features of the vascular system they approach the higher forms and depart from fishes, e.g. in the presence of an auricular septum, of an inferior vena cava, of a branch of a posterior vascular arch to the lung sacs, in the fact that in the adults of the higher forms branchial structures are not present on the vascular arches, that the vascular arches tend not to be connected with each other dorsally, and in the differentiation in the higher forms of the right systemic arch from the left. But with regard to these features it must be noted that the first three are already found in *Dipnoi*, and that the others are only characteristic of the higher members of the *Amphibia*.

The heart is contained in the pericardial sac and is typically five-chambered, consisting of sinus venosus, two auricles, a single ventricle and a conus arteriosus (bulbus cordis). The chambers are more compacted together than in fishes, the sinus venosus being placed more forward on the dorsal side of the auricle. The left auricle is smaller than the right and the interauricular septum is incomplete in Urodeles and *Gymnophiona*, complete in *Anura*. The sinus venosus opens into the right auricle, and the pulmonary veins into the left. All the chambers of the heart are rhythmically contractile. Except at its base the cavity of the ventricle is broken up by muscular strands, so as to present a spongy character and its wall is without blood vessels. The conus arteriosus is spirally twisted and usually possesses a longitudinal valve, the attachment of which lies along the axis of the

spiral. There are two valves at the junction of the sinus and right auricle, and two considerable valves at the margin of the combined auriculo-ventricular apertures (Fig. 158). The latter are held to the ventricular wall by cords, and there may be two smaller additional valves. The auricles open into the left side, and the conus arises from the right side of the ventricle, and from that portion of it which is free from muscular strands (Fig. 158). There is a row of three, sometimes four, semilunar valves at each end of the conus (Fig. 157). The conus arteriosus leads into a short ventral aorta (truncus arteriosus) which in

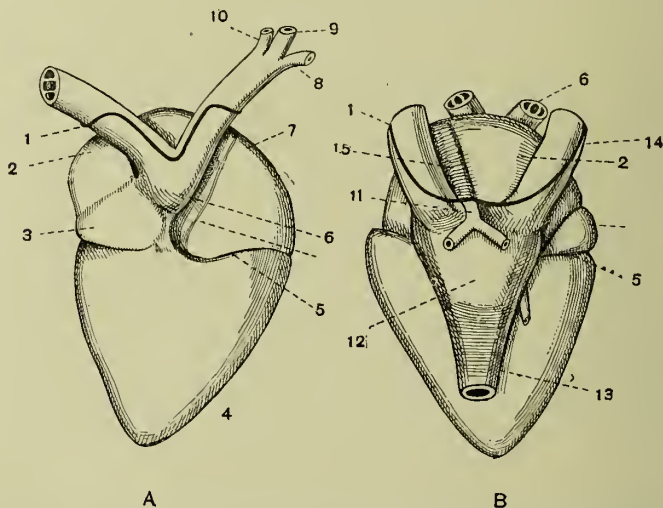


FIG. 155.—A ventral, B dorsal view of the heart of a frog (after Gaupp). 1 line marking the anterior limit of the pericardium; 2 right auricle; 3 conus arteriosus (bulbus cordis); 4 ventricle; 5 sulcus coronarius marking the junction of the auricles and ventricle; 6 truncus arteriosus; 7 left auricle; 8 pulmo-cutaneous artery; 9 aorta; 10 common carotid; 11 pulmonary vein; 12 sinus venosus; 13 inferior vena cava; 14 right superior vena cava; 15 left auricle.

the *Anura* is divided into a dorsal and ventral chamber by a horizontal partition. The branches of the ventral aorta are bound together for a short distance in a common sheath.

In the *Gymnophiona* the conus is short, not spirally twisted, is without a longitudinal valve, and in some species has only one row of valves. In other *Amphibia* there is a row of valves at each end. In *Proteus* and *Menobranchus* it is straight and without the longitudinal valve. The longitudinal valve presents considerable variations, e.g. in the genus *Triton* it may be present, or absent, or made up of a row of small processes. a condition which suggests that it is really composed, as it is in *Dipnoi*, of a row of small semilunar valves. It begins posteriorly close to one of the



valves which guard the ventricular end of the conus and is continuous with the convex posterior side of the right hand valve of the three (or four) valves which guard its anterior end (Fig. 156). It is attached in the main to the dorsal wall of the conus and projects freely into it, reaching half or two-thirds of the way across it. Its line of attachment lies in the axis of the spiral into which the conus is twisted. In *Salamandra* (Fig. 157) the branches of the ventral aorta, which are continued as the arterial arches, are connected by a common sheath and are given off as explained in the following description. The ventral aorta is undivided posteriorly (Fig. 157), but in front it is divided by a horizontal septum into two compartments of which the ventral is again divided by three vertical partitions, which do not however reach the hind end of the horizontal septum, into four canals. Of these the two median are continued into the anterior (carotid) arches (*I*), and the lateral into the second (aortic) arches (*II*). The dorsal division is divided by a vertical septum into two, each of which

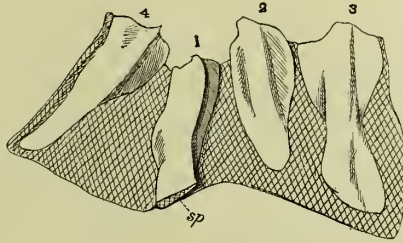


FIG. 156.—The conus of *Salamandra maculosa* laid open (after Boas), showing the four rather long semilunar valves of the anterior row, of which that marked 1 is continued backwards as the longitudinal valve (*Sp*). When only three valves are present, the valve marked 4 is absent.

is continued as the at first conjoined third and fourth arches (*IV*).

In *Rana* and its allies the conus has three semilunar valves at each end. The longitudinal valve (Fig. 158) begins on the ventricular side of the ventricular opening near the right semilunar valve; its line of attachment, running across the ventral side of the conus, passes on to its left wall and then on to the dorsal wall, ending in front in the right hand

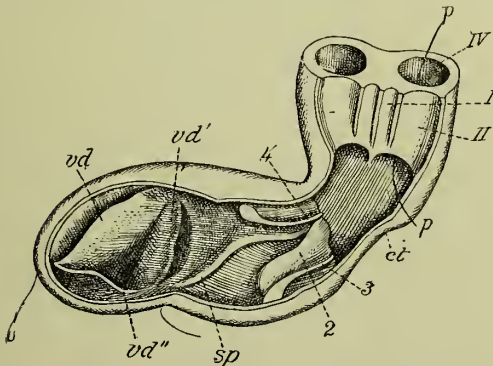


FIG. 157.—Conus and ventral aorta of *Salamandra maculosa*; a piece of the ventral wall has been removed (after Boas). The ventral aorta is slightly diagrammatic. *I, II, IV*, divisions of the ventral aorta or roots of the arterial arches, *I*, the carotid, *II*, the systemic, *IV*, the conjoined third and fourth (pulmonary). *p p*, a bristle inserted into *IV*; *α*, limit between the conus and ventral aorta (points a little too high up); 2, 3, 4, three valves of the distal row corresponding to those similarly numbered in Fig. 156; *sp*, longitudinal valve; *vd*, *vd'*, *vd''* valves of posterior row.

valve (No. 1) of the anterior row as described for *Salamandra*. It incompletely divides the conus into two chambers, of which the right hand one is called the cavum aorticum (Fig. 159), the other the cavum



pulmo-cutaneum. The position of these is reversed at the ventricular opening (where the valve is attached ventrally), the cavum pulmo-cutaneum being on the right and the cavum aorticum on the left. Inasmuch as the longitudinal valve runs to the right valve on the right side of the ventricular opening, it is clear that the cavum pulmo-cutaneum, which at this point is, as above described, on the right side of the conus, does not lead into the ventricular opening but is cut off from it by the longitudinal valve (Fig. 158). The cavum aorticum on the other hand leads behind right into the ventricle. The result of this arrangement is that when the conus becomes functionally divided into two chambers, as it does when it contracts, and the free edge of the longitudinal valve meets the opposite wall, the cavum pulmo-cutaneum is completely cut off from the ventricle and ends blindly.

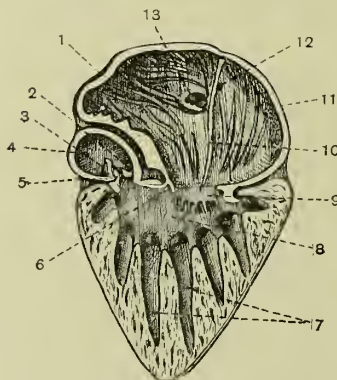


FIG. 158.—Heart of *Rana* opened by a longitudinal horizontal section, ventral view of the dorsal half (after Gaupp). 1 right auricle; 2 dorsal, 5 right of the three proximal valves of the conus; 3 longitudinal valve of the conus; 4 conus arteriosus; 5 see above; 6 right auriculo-ventricular valve; 7 spongy part of ventricle; 8 clear central space of ventricle; 9 dorsal auriculo-ventricular valve; 10 interauricular septum; 11 left auricle; 12 ostium venae pulmonalis; 13 ostium sinus venosi.

2 and 3 (Fig. 160, A, a). The result of this arrangement is that the ventral aorta is completely divided into two passages of which the dorsal (pulmonary) opens behind into the cavum pulmo-cutaneum of the conus (left), the opening being guarded by valve No. 2 and one half (1b, dorsal) of the divided valve No. 1, while the ventral passage (carotid and aortic) leads into the cavum aorticum with valve No. 3 and the other half (1a) of valve No. 1. It is further to be noted, and this is a highly interesting point, that the two carotid arches open by a common opening into the right aortic arch (Fig. 159), thus foreshadowing the arrangement found in Reptiles.

The object of these elaborate arrangements in the conus and ventral aorta of the higher *Amphibia* is to ensure a proper distribution of the pulmonary and venous blood along the outgoing arteries. In the Urodeles

Anteriorly the longitudinal valve is connected (Fig. 159) with valve No. 1 (the valve on the right side of the anterior end of the conus), which is very large and extends right across the conus, so that the middle point of its free edge is attached to the opposite wall (left) of the conus between the other two valves (2 and 3) (Fig. 160, A, a). Turning now to the ventral aorta, we find that the horizontal septum, which in *Salamandra* divides it anteriorly into a ventral portion continuous with the carotid and aortic arches, and a dorsal portion continued into the pulmonary arches (Fig. 157), here reaches back to the hind end of the ventral aorta (Fig. 159), and is attached posteriorly to the inner (concave) surface of the valve No. 1 (*trs*, Fig. 160). The left hand side of the hind end of this septum is attached to the valve at the point where the latter is fused with the left hand wall of the conus between valves

in which the longitudinal valve of the conus and the horizontal septum of the ventral aorta are less developed, no separation of the arterial (pulmonary) blood from the systemic venous blood is possible; the two must undergo complete admixture in passing through the ventricle, conus and ventral aorta. In the *Anura* however this is not the case. In these animals the anatomical arrangements are of a nature to ensure that the pulmonary arteries receive purely venous blood, the mixed and purely arterial blood being directed into the aortae and the carotids. It is further said that the carotids receive more purely arterial blood than the systemic

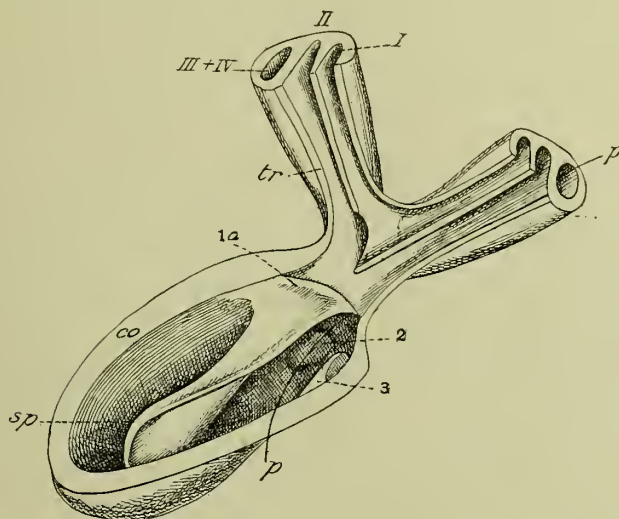


FIG. 159.—Conus and ventral aorta of *Rana platyrhina*, opened along the [ventral] side ventral aorta slightly diagrammatic (after Boas). I, II, III—IV roots of the aortic arches, carotid, aortic, and pulmonary (III—IV); p p bristle inserted from the conus into orifice of the pulmonary, it passes dorsal to the horizontal septum of the ventral aorta through the opening guarded by valve No. 2 and 1b; 2 valve No. 2 of anterior row; 3 valve No. 3 of anterior row; 1a ventral half of valve No. 1 which with 3 guards the entrance into the ventral division of the ventral aorta which has been laid open; the other half of this valve 1b is not shown; the attachment of 1a to the left hand wall of the conus is between valve 2 and 3; this is not clearly shown in the figure; co conus; sp longitudinal (spiral) valve of conus; tr ventral aorta (points a little too far up). The hind end of the conus where the attachment of the longitudinal valve becomes ventral is not shown.

aortae; this may be true, but it is not quite so clear from the arrangements how it is effected.

The ventricular cavity is, except at its base where the auricles and conus open, broken up by muscular bands so as to assume a spongy character. This prevents the mixture of venous and arterial blood which is poured in from the auricles. The blood which enters from the right auricle is venous, and this is discharged into the right side of the ventricle from which the conus arises; consequently the blood which flows into the conus during the first phases of the ventricular systole will be venous. This will distend the conus and fill both chambers into which it is imperfectly divided by the longitudinal valve, and passing forward along the cavum pulmo-cutaneum will also fill the pulmonary arteries which are

empty and interpose much less resistance to the entry of blood than do the aortic and carotid arteries (as will be explained in a moment). In the second phase of the ventricular systole, the conus itself contracts and the free edge of the longitudinal valve becomes applied to its ventral wall, whereby its cavity becomes converted into two separate chambers. Of these the *cavum pulmo-cutaneum* is closed behind so that no more blood can enter it from the ventricle; but it remains open in front to the dorsal division of the ventral aorta and so to the pulmonary arteries. The result of the contraction of the conus upon the *cavum pulmo-cutaneum* will be to empty it and to drive the blood through the pulmonary arteries, thus rendering easy the entrance of blood into these structures at the next ventricular systole. The *cavum aorticum* on the other hand remains open to the ventricle during the second phase of the ventricular systole. It contains probably a certain amount of venous

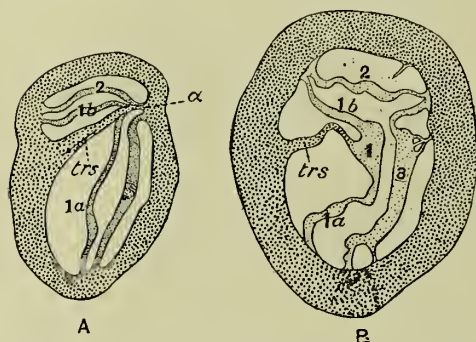


FIG. 160.—Two transverse sections through the conus of *Rana platyrhina*. A at the junction of the conus and ventral aorta; B a little further back (after Boas); a the point where valve No. 1 is fused with the left wall of conus; 1b dorsal part, 1a ventral part of valve No. 1; 2 dorsal, 3 ventral of the three valves of the anterior row; trs, horizontal septum of the ventral aorta. The sections are viewed from the front side. The longitudinal valve of the conus is not shown, but if posterior sections were represented, it would appear as a continuation of valve 1b and 1a, the pocket of this valve with the horizontal septum trs disappearing.

blood already driven into it and receives now all the rest of the ventricular blood, namely, that from the left side. This must be largely arterial, for most of it must have entered the ventricle from the left (pulmonary) auricle. This blood, together with the venous blood already in the *cavum aorticum*, must be entirely delivered through the *cavum aorticum* into the ventral division of the ventral aorta, and so into the carotid and systemic arteries. The question now arises whether there is any arrangement whereby this blood is sifted and the most arterial of it sent into the carotid arteries. It is said that observation has shown that the carotids receive more purely arterial blood than the systemic aorta. The following structural features have been alleged as contributing to this, from a physiological point of view desirable, result. The three arches of the left side lie in a line with the conus and ventral aorta, the arches of the right side passing off at an angle (Fig. 159). The effect of this will be that the blood in order to enter the right aortic arch and the two carotids, which as we have seen come off from this arch, will have to pass round a corner. It will be easier therefore for it to flow straight on into the left systemic arch. In this way it is possible that the first blood from the *cavum aorticum*, i.e. mixed venous and arterial, will pass into the left arch, leaving only the last blood which enters the conus, i.e. as we have shown the most purely arterial, to enter the right arch and the carotids. It has further been alleged that the carotid glands (described below) interpose ad

blood already driven into it and receives now all the rest of the ventricular blood, namely, that from the left side. This must be largely arterial, for most of it must have entered the ventricle from the left (pulmonary) auricle. This blood, together with the venous blood already in the *cavum aorticum*, must be entirely delivered through the *cavum aorticum* into the ventral division of the ventral aorta, and so into the carotid and systemic arteries. The question now arises whether there is any arrange-

ditional resistance to the entrance of blood into the carotid arteries, so that no blood enters them until the systemic arteries are full. Lastly, we must mention the fact that there is in each systemic aorta, at the point where it diverges from the carotid and pulmonary, a small semilunar valve, so arranged as to interpose resistance to the flow of blood into the aorta. It is difficult to see how this paradoxical valve (*valvula paradoxa* as it has been called by Gaupp) assists in sifting the blood of the cavum aorticum, but it may be of use, as probably the carotid gland is of use, in preventing the venous blood which enters the conus in the first phase of the ventricular systole from passing into the systemic aortae.

To summarize the whole matter: the first blood which enters the conus is purely venous and passes mainly into the pulmonary arteries in which the resistance is less than in the systemic and carotids, partly because the pulmonary arteries are empty and ready to receive it and partly because of the resistance of the *valvula paradoxa* and carotid glands;

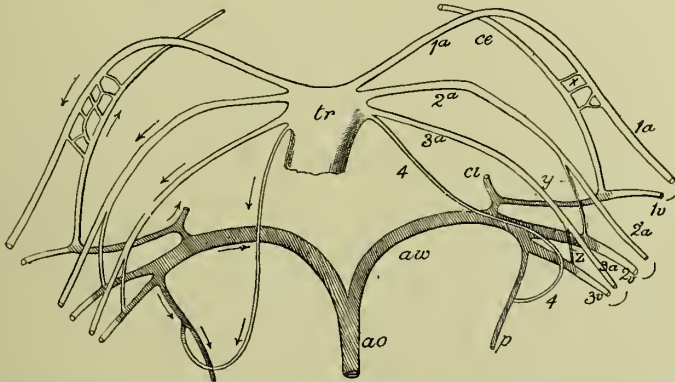


FIG. 161.—The arterial arches of a larval salamander slightly diagrammatic (after Boas). 1a-3a the three branchial arteries (afferent branchial vessels); 1v-3v the corresponding branchial veins (efferent vessels); 4 the fourth arterial arch; ao dorsal aorta; aw root of dorsal aorta; ce external carotid; ci internal carotid; p pulmonary artery; tr ventral aorta; x anastomosing vessels between external carotid and first afferent branchial vessel; y, z, anastomosing vessel between the afferent and efferent vessels of the second and third branchial arches.

the last blood which enters the conus is unable to pass into the pulmonary because the cavum pulmo-cutaneum is entirely cut off from the ventricular orifice by the longitudinal valve. The first of this blood together with the previously-arrived venous blood, i.e. mixed blood, enters the left systemic arch because this is easiest of access, being in a straight line with the conus and ventral aorta. This blood is distributed mainly to the visceral arteries (see below). The last blood, i.e. the most purely arterial, will enter the right arch and the carotid arteries which leave the right arch. This blood is distributed to the head and the posterior part of the body (exclusive of the viscera). The *valvula paradoxa* being a small single valve will cease to act as a serious obstruction as soon as the artery becomes sufficiently distended to allow of the blood passing it. If this account is correct it is clear that the systemic arches are differentiated functionally in the *Anura* as they are in the *Reptilia*. The left arch receives mixed blood which is mainly sent to the viscera, the right arch receives purely arterial blood which is sent to the head and posterior



part of the body; the principal functional difference being that in *Amphibia* the left subclavian is in connection with the left systemic arch, whereas in *Reptilia* it comes off from the system of the right arch.

Four arterial arches are developed in the *Amphibia*, the first, second, third and fourth branchial. In addition to these the ventral aorta of the larva sends a branch to the hyoid which however is usually incomplete, not reaching the dorsal system; in all cases it eventually atrophies. The vascular arches of the larval salamander are shown in Fig. 161. The ventral aorta gives off four branches on each side. Of these the first three pass to the first three branchial arches and supply their gills. They may consequently be described as consisting of an afferent (branchial artery) and an efferent (branchial vein) portion united

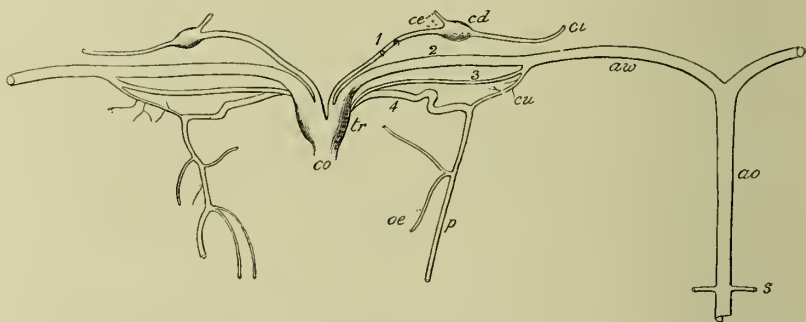


FIG. 162.—Arterial arches of an adult *Salamandra maculosa* (after Boas). 1, 2, 3, 4 the four branches of the ventral aorta (vascular arches); ao dorsal aorta; aw root of dorsal aorta; ce external carotid; ci internal carotid; co conus arteriosus; cu ductus Botalli of pulmonary arch; p pulmonary artery; oe oesophageal branches of p; s subclavian artery; tr ventral aorta.

by the vessels in the gills. In addition to these connections the afferent and efferent vessels of the second and third branchial arches are directly connected by anastomosing vessels (*y*, *z*). The first afferent vessel is not so connected with its branchial vein, but fine anastomosing vessels (*x*) pass between it and the external carotid (*ce*, lingual) which is a branch of the first efferent vessel. Further dorsally the first efferent vessel gives off the internal carotid (*ci*). All the efferent vessels fall into the dorsal aorta. The fourth vascular arch is not connected with a gill; it is a slender vessel running in the fourth branchial arch. Dorsally it gives off the pulmonary artery and joins the efferent vessel of the third arch; of which indeed the pulmonary artery has the appearance of being a branch.



In the adult salamander the arrangement is shown in Fig. 162. The ventral aorta has four branches (for the exact way in which they come off see below). The gills have disappeared and the afferent and efferent limbs of the vessels are continuous. The first arch has become the carotid and has lost its dorsal connection with the second. The second arch has become the arch of the aorta (systemic arch); the third remains as a small vessel joining the second dorsally, but in some individuals it appears to be absent; the fourth is continued as the pulmonary artery, but retains its dorsal connection (ductus arteriosus or Botalli) with the preceding arches

In *Triton* the third arch has disappeared in the adult, and the first arch (carotid) retains its dorsal connection with the second. In *Proteus* and *Menobranchus* the fourth vascular arch is not present in the adult, and the pulmonary is a branch of the third, the ventral end of which is conjoined with that of the second.

In *Siren* four arches are present and the arrangement is similar to that in the larval salamander. In all the Perennibranchiates the relation of the gills to the arches is similar to that found in the salamander larva.

In the *Anura* \* the third arch is completely absent in the adult, though present in the larva. The pulmonary artery is a branch of the fourth, and the first and fourth arches are not usually connected with the dorsal system. The **Carotid Gland** is a plexus of small vessels inserted in the course of the carotid artery. It is not derived from a gill as was formerly supposed, but from the vessel which directly connects the efferent and afferent limbs of the first branchial arch in the older larva. This vessel becomes plexiform and together with some epithelial tissue derived from the first branchial cleft gives rise to the carotid gland.

Of the rest of the arterial system there is not much to be said. The frog may be taken as typical, with one exception, viz. that the visceral arteries are all gathered up into one, the coeliacomesenteric, which leaves the left aortic arch close to its union with the right. Almost all the blood of the left aortic arch of the *Anura* goes into this vessel, the continuation of it to the dorsal aorta being very small. In the Urodeles the visceral arteries come off as many branches from the dorsal aorta. There are two superior venae cavae (ductus Cuvieri) made up by the junction of the jugulars (anterior cardinals) and the subclavians, and an inferior vena cava which arises in the kidneys. The venous blood of the hind end of the body is all sent either through

\* For an account of the development of the vascular arches of the frog, see A. M. Marshall, "*Vertebrate Embryology*," London, 1893.

the kidney to which it is taken by the renal-portal veins or through the liver by the anterior abdominal vein. Vertebral (azygos) veins are very generally present, opening into the superior venae cavae.

The question of the homology of the inferior vena cava with the piscine veins is difficult to settle. From its relations to the kidneys and from the condition in *Dipnoi*, it would appear to be one or both of the posterior cardinals. The difficulty in the way of this view is that it does not, so far as is known, develop from the posterior cardinals which are always present in the embryo.

In *Proteus* and *Siren* some of the pulmonary blood is returned into the vena cava inferior (Hyrtl).

The red blood corpuscles are nucleated. They are oval in shape and of considerable size, reaching in *Amphiuma* in their greatest diameter  $\frac{1}{4}$ th mm.

The lymphatic system consists of vessels and sinuses. There is a large subcutaneous lymph sinus, especially well developed in the *Anura*, and a large subvertebral sinus enveloping the aorta, kidneys, etc. The lymphatic vessels open into the great veins, and near the point of opening are often dilated into muscular contractile chambers, the lymph-hearts. In the frog there are two pairs of these; a posterior pair placed near the hind end of the urostyle and opening into the femoral veins, and an anterior beneath the suprascapulae and opening into the subscapular veins. In the Urodeles the posterior pair alone is present. There are no lymphatic glands along the course of the vessels as in birds and mammals, but patches of lymphatic tissue, in which amoeboid cells are set free, are present in different parts of the body.

A spleen, usually placed in the mesentery near the stomach, is present.

The **Urinogenital Organs** \* are constructed on the same type as those of Elasmobranchs. The kidney is an elongated gland (except in *Anura*) with persistent nephrostomes and with a duct to which the collecting tubules pass. In the male there is a testicular network, through which the sperm passes from the testis to some of the kidney tubules. The kidney duct serves therefore as vas deferens as well as ureter. It opens

\* Spengel, J. W. *Arbeiten a.d. Zool. Inst. Würzburg*, 3, 1876, p. 1.  
Brauer, A. "Entwick. der excretionsorgane der Gymnophionen," *Zool. Jahrb. (Anat.)*, 1902, 16, p. 1.

posteriorly into the side of the cloaca. In the female the müllerian duct forms the oviduct; its abdominal opening is far

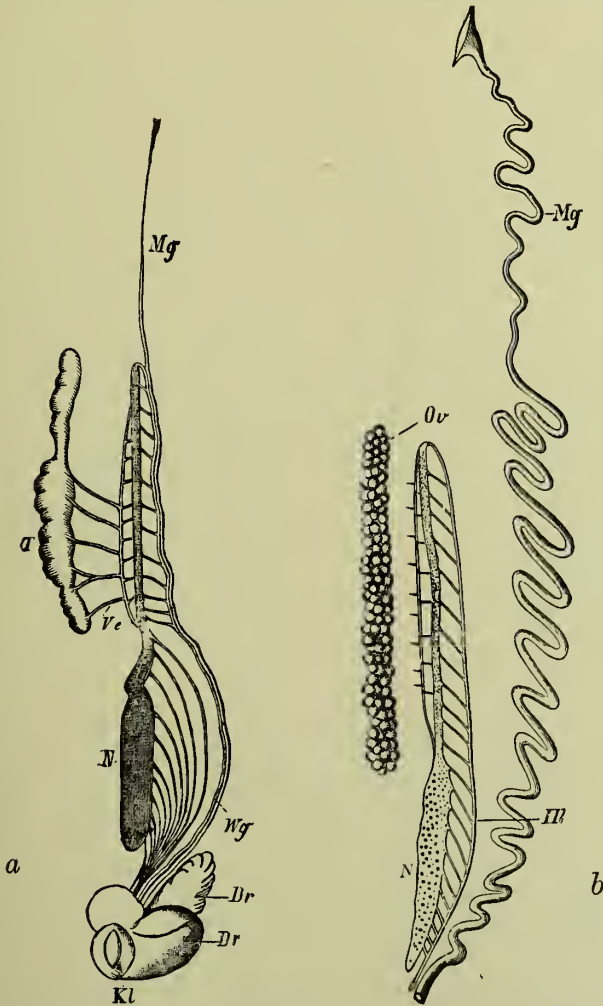


FIG. 163.—Urinogenital organs of the left side of *a* a male, and *b* a female salamander, partly diagrammatic (from Claus). *Dr* prostate glands; *Wg* longitudinal (mesonephric) duct of the kidney; *Kl* cloaca; *Mg* oviduct; *N* kidney with collecting tubules passing to the longitudinal duct; *Ov* ovary; *T* testis; *ve* vasa efferentia; *Wg* longitudinal (mesonephric) duct of the male.

forward, and posteriorly it opens laterally into the cloaca. It generally persists as a vestige in the male. The cloaca possesses a vesicular ventral appendage—the cloacal or allantoic bladder

which is not found in fishes and into which the urinary ducts do not open as they do in mammals. There is no copulatory organ (though in the *Gymnophiona* the cloaca can be extruded and used as such). There is a lobed fat-body frequently connected to the front end of the generative gland. There is always a functional pronephros in the larva which atrophies in the adult.

In the salamander or newt, which may be taken as type, the kidney is much narrower in front than it is behind (Fig. 163). The narrower, anterior portion may be called the sexual part, because in the male the testis is connected with it by the testicular network. It is also sometimes called the *mesonephros* because it corresponds roughly to the mesonephros (Wolffian body) of the embryos of the *Sauropsida* and *Mammalia*. In this case the posterior thicker portion might be called the *metanephros*, on the view that it corresponds to the permanent kidney of the higher types. The duct runs by the side of the gland and receives the collecting tubes. In the male the collecting tubes of the metanephros are inclined backwards and all join to open at one point into the longitudinal duct close to the cloaca (Fig. 163 *a*). An incipient ureter is thus formed. In this case the longitudinal duct is mainly associated with the anterior sexual part of the kidney or mesonephros and is for that reason frequently spoken of as the *mesonephric duct* (Leydig's duct).

The renal tubules (nephridia) consist of four parts, (1) the collecting tubule, which is continuous in the kidney with (2) the contorted tubule which is the especially glandular part, and passes into (3) the malpighian body, from which passes (4) the peritoneal canal to the body-cavity opening (nephrostome) placed on the ventral surface of the kidney (Fig. 164). The contorted tubule and peritoneal canal usually join before opening into the malpighian body (Fig. 164 *mk'*). Such a tubule is called a primary or simple tubule. The anterior part of the kidney (*mesonephros*) of Urodeles consists entirely of such primary tubules. In the metanephros however we find compound tubules. These consist of primary tubules each with its nephrostome, and of a number of dorsally placed secondary tubules (also with nephrostomes) which open into the collecting part of the primary tubule. The primary tubules are not arranged segmentally in any Amphibian, except the *Gymnophiona*. The number of primary tubules in a segment is greater in the posterior than in the anterior part of the kidney. The testicular network or connection between the testis and mesonephros is constructed as follows (Fig. 163). There is a longitudinal duct, called the longitudinal duct of the testis (not shown in fig.), running along the base of the testis and receiving the testicular tubules. This gives off an irregular number of canals—the vasa efferentia—which

pass into a second longitudinal canal (Fig. 163) placed near the mesonephros and called the longitudinal canal of the mesonephros (absent in *Spelerpes*, *Batrachoseps*, etc.). This sends off transverse canals, which correspond in number with the primary renal tubules in the part of the kidney involved in the testicular connection and open into the malpighian bodies of these tubules. So that the sperm passes through the renal tubules of the mesonephros into the mesonephric duct. The nephrostomes of these sexual tubules atrophy in the adult of all male Urodeles except *Spelerpes*; but are present in this region in the young form and in the female. The sexual part of the kidney varies much in length. In *Siredon* as many as 32 primary tubules are connected with the testis. It is much reduced in *Spelerpes*. A vestige of the müllerian duct is generally present in male *Amphibia*; and rudiments of the testicular network can frequently be detected in the female (Fig. 163 *b*). The collecting tubules of the metanephros are directed backward and join into one or more short ducts (ureter) before opening into the mesonephric duct. In *Batrachoseps* the first collecting tube is specially developed and receives all the other collecting tubes of the metanephros. In the female of all Urodeles and in the males of *Proteus*, *Menobanchus* and *Siren* the collecting tubes retain their transverse course and open direct into the mesonephric duct. In rare cases the ureter opens direct into the cloaca.

In the *Gymnophiona* the kidney is narrow and elongated, extending almost the whole length of the body cavity. The primary tubules are segmentally arranged, but many of them become compound in the adult. There is but little indication of differentiation into meso- and metanephros, and the testicular network is joined to the kidney some little distance behind its front end (Fig. 165). The nephrostomes both of the sexual and non-sexual part of the kidney persist in the adult.

In the *Anura* the kidney is compact, and the sexual part is not marked off from the rest. There is a testicular network which in *Bufo*, etc., is connected with some of the malpighian bodies (Fig. 166). In *Rana* the transverse canals which leave the longitudinal canal of the mesonephros, pass through the kidney and open into the collecting tubes of the renal tubules. In *Bombinator* the longitudinal canal runs through the kidney and opens into the anterior end of the kidney duct which curves round the front end of the kidney; the transverse canals end blindly in the substance of the kidney. In *Discoglossus* a canal arises from the front end of the testis and passes round the front end of the kidney to be continued into the anterior end of the ureter. This canal appears to be the only representative of the testicular network. In *Alytes* the arrangement is very peculiar and differs from that of all other *Anura* (Fig. 167). There is a ureter (fused metanephric collecting tubes) passing out from the hind

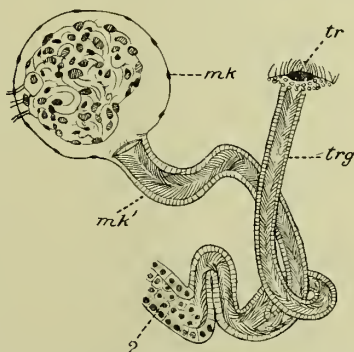


FIG 164.—Malpighian body and nephrostome of a kidney tubule of *Proteus* (after Spengel). *tr*, Nephrostome; *trg*, peritoneal canal; *mk* malpighian body, and 2 beginning of contorted tubule of the sexual part of the kidney; *mk'* stalk of malpighian body.



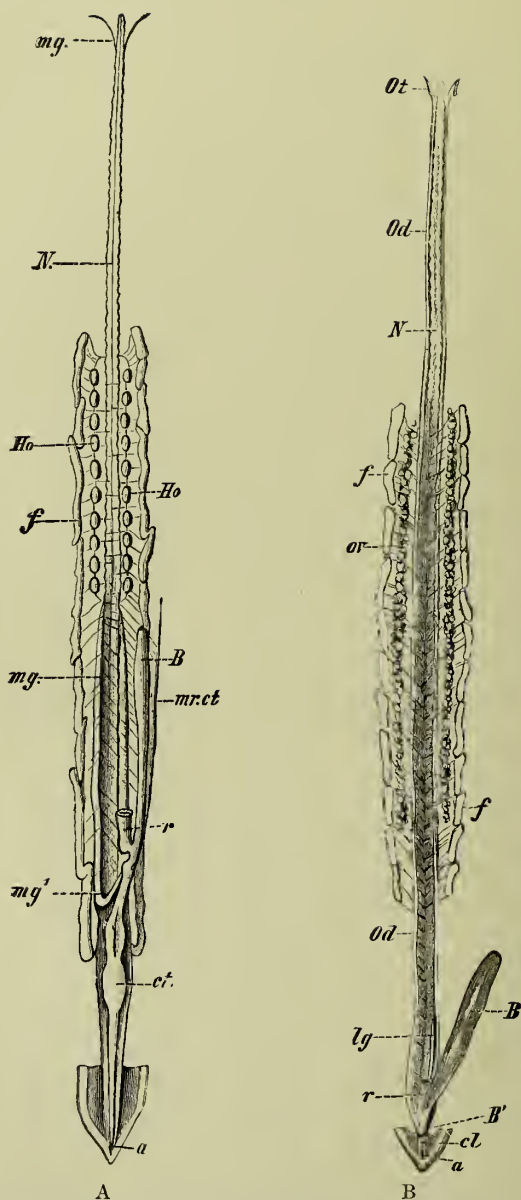


FIG. 165.—Urinogenital organs of *Epicrion glutinosum*. A male; B female (after Spenge from Wiedersheim). *a* anus; *B* bladder; *B'* appendage of bladder; *cl*, *cl* cloaca; *f* fat body; *Ho* testis; *lg*, kidney duct; *mg*, *mg'* müllerian duct in male; *od* müllerian duct (oviduct) in female; *mr*, *ct* retractor muscle of cloaca; *N* kidney; *Ot* abdominal opening of oviduct; *ov* ovary; *r* rectum.

end of the kidney and joining the mesonephric duct (Leydig's duct). The latter is continued forwards beyond the kidney ending blindly in front; and receiving a small testicular network which passes from the testis round the front end of the kidney and is entirely disconnected from the kidney. This would appear to be an extreme modification of the condition characteristic of Urodeles, the sexual part of the kidney having been entirely aborted.

In the *Anura* nephrostomes are present, but it is doubtful whether they open into the kidney tubules in the adult. It has been asserted\* that they open into the renal veins. This statement must be accepted with caution. It appears more probable that they have lost their connection with the renal tubules and persist as ciliated cups on the surface of the kidney.

Bidder's organ is found in *Bufo* as a structure attached to the front end of the generative gland. In both sexes it consists of an aggregation of immature ova.

The fat-body consists of lymphatic tissue with fat in the meshes. It appears to be a reserve of nutriment which is drawn upon when the sexual glands are becoming mature.

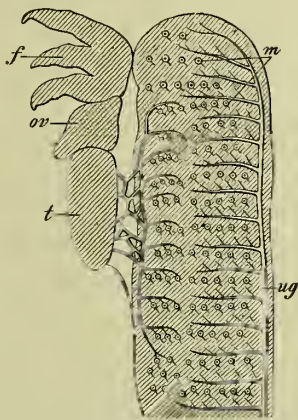


FIG. 166.—Urinogenital system of male *Bufo* (after Spengel). *f* fat body; *m* malpighian body; *ov* Bidder's organ (ovary); *t* testis; *ug* duct of kidney.

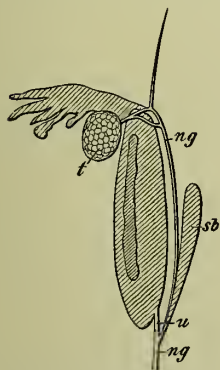


FIG. 167.—Urinogenital system of *Alytes obstetricans* (from Gegenbaur, after Spengel). *t* testis; *ng* longitudinal duct of kidney (mesonephric); *sb* seminal vesicle; *t* testis; *u* ureter (after Spengel, from Gegenbaur).

The **Suprarenal** bodies are small yellow structures on the ventral surface of the kidneys in the *Anura*, on their median side in *Urodela*.

The oviducts open separately into the cloaca, except in *Hyla*, *Bufo* and *Alytes*, in which the opening is median. They receive through their abdominal opening the eggs, which are dehiscent into the body-cavity. They are usually more or less convoluted, possess 'glandular walls' which secrete an albuminous covering for the eggs, and they are frequently dilated into a receptacle in which the eggs are collected, close to their cloacal opening.

\* E. J. Bles, *Proc. Cambridge Phil. Soc.*, 9, 1898.

Males and females are often distinguished by their size and colour, and also by other peculiarities (vocal sacs, dorsal crests, etc.) which are specially prominent at the breeding season. In spite of the absence of organs of copulation, sexual intercourse takes place, but it usually consists merely of an external approximation of the two sexes (*Anura* in which the male embraces the female from the back), and results in the fertilisation of the eggs outside the body of the mother. In cases in which the spermatozoa are introduced into the female generative tracts, spermatophores are formed, probably by the cloacal glands, and introduced into the female cloaca by the application of the swollen lip of the male cloaca to the anus of the female (Salamandrines).



FIG. 168.—*Alytes obstetricans*.  
Male, with the string of  
eggs. (from Claus).

In such cases the eggs may undergo their development within the oviduct, and the young be born at a more or less advanced stage of development (*Salamandra maculosa*, *S. atra*, *Spelerpes fuscus*, etc.). It is only exceptionally that the parents have an instinct to watch over the further fate of their brood, as for example in *Alytes* (Fig. 168) and the Surinam toad (*Pipa dorsigera*). The male of *Alytes* winds the strings of eggs round its hind legs and burrows into the damp earth, and only gets rid of its load when the embryonic development is completed. In *Pipa* the eggs are placed on the back of the female, which then develops a cell-like pouch round each egg. In this case the whole development takes place in the egg. In *Noto-trema* the eggs are conveyed into a spacious brood pouch beneath the dorsal integument, in which the eggs undergo their embryonic or their whole development. In *Rhinoderma* the eggs are placed in the enlarged vocal sacs of the male, where they undergo the whole of their development. In these cases the eggs are large so that the young can undergo the whole or part of their later development in the egg. This is the case also in some forms in which the eggs are deposited in damp situations and the young are not hatched until after the loss of the gills (*Arthroleptis seychellensis*, *Rana opisthodon*, *Hylodes martinicensis*, etc.). When the eggs are relatively small, they are usually laid in

water, either singly and attached to water plants (e.g. newt), in clumps (e.g. frog), or in strings (e.g. toads) ; but in some cases they are deposited out of the water, in situations in which the larvae can easily reach it.

**Development.\*** The eggs, which possess a considerable amount of food yolk, are relatively small, and undergo (except in the *Gymnophiona*) a total, but unequal segmentation (Fig. 169). A gastrula is formed by a modification of the process of invagination, and the blastopore in some cases (e.g. newt) persists as the anus and in some cases (e.g. frog) closes up, the anus being a later perforation on its site. A neurenteric canal is very generally present. An amnion and allantois are not formed, though a cloacal bladder, an organ homologous with the allantois, arises as a median ventral diverticulum of the cloaca. The embryos

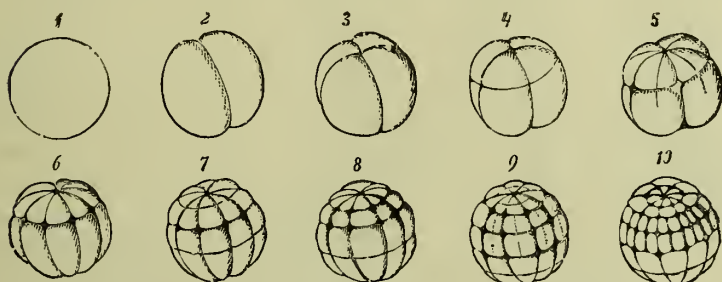


FIG. 169.—Unequal segmentation of the frog's egg in ten successive stages (after Ecker).

are also without any external yolk-sac constricted off from the body, the yolk being enclosed at an early period by the side-walls of the body. With a few exceptions, which have already been referred to and are mentioned again in the systematic part, the young leave the egg in an immature condition and undergo the later part of their development as free-swimming larvae.† In the *Anura* these larvae are generally known as tadpoles. The larvae are always aquatic and breathe by gills (see p. 278) and possess other larval organs, e.g. a pronephros, and lateral line sense organs. Their vascular system is on the piscine type which gradually gives place to that characteristic of air-breathing

\* Balfour, *Comparative Embryology*, vol 2, 1883. Marshall, *Vertebrate Embryology*, 1893, Brauer, *op. cit.*

† The resemblance in certain cranial characters between the anuran larva and the marsipobranchii has already been referred to (p. 96).

forms (p. 289) as the lungs develop. In the so-called perenni-branchiate forms the gills and lateral line persist, either partly or throughout life, but the pronephros always gives place to the kidney. In some cases the larvae actually become sexually mature (paedogenesis, p. 280). In the *Anura* the larval organs are more conspicuous and the final change by which the aquatic tadpole becomes a terrestrial animal is so striking as to be called a metamorphosis. The tadpole possesses two suckers (Fig. 170, *S*) on the ventral surface behind the mouth, which however disappear

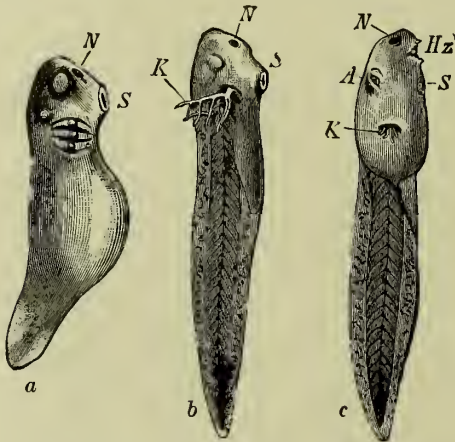


FIG. 170.—Larval stages of the frog (after Ecker). *a*, embryo some time before hatching, with wart-like gill papillae on the branchial arches. *b*, larva some time after hatching with external gills. *c*, older larva with horny beak and small branchial clefts beneath the integumentary operculum, with internal gills. *N* nasal pit; *S* sucker; *K* external gills; *A* eye; *Hz* horny tooth.

quite early in larval life (similar suckers are present on the throat of *Triton* larvae, where however they are stalked). It also possesses a horny beak (*Hz*) on each lip which is lost at the metamorphosis. Moreover the caudal region of the body is represented by a well developed laterally compressed tail, which is gradually absorbed after the animal has become terrestrial, and the limbs functional. The limbs develop during

larval life: the anterior limbs are formed beneath the opercular fold and only appear at the metamorphosis, when that membrane is shed; the posterior limbs develop at the side of the anus and are visible from their first appearance as buds. The operculum develops early in larval life as a cutaneous fold from the hyoid arch which gradually grows back over the gills and gill-slits, causing the atrophy of the external gills (Fig. 170). A branchial chamber is thus formed between the fold and the body, into which the gill-slits open. These chambers at first open widely behind, but very soon the openings narrow. In the *Aglossa* both openings persist and are lateral in position. In the *Disco-*



*glossidae* the openings converge and combine into one median ventral opening. In other *Anura* the right opening passes on to the left side and combines with the left, so that there is only one spiracle, as these openings are called, on the left side of the body.

The intestine of the tadpole is long and spirally coiled. At the metamorphosis the animal undergoes an ecdysis, with which is connected the appearance of the anterior limbs, the closure

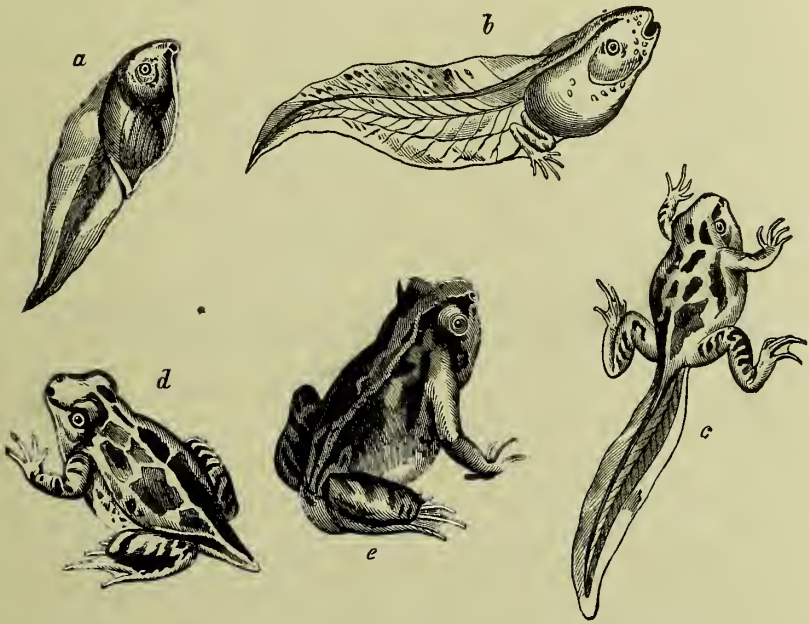


FIG. 171.—Later stages in the development of *Pelobates fuscus*. *a*, larva without limbs, with well-developed tail. *b*, older larva with hind limbs, *c*, larva with two pairs of limbs. *d*, young frog with caudal stump. *e*, young frog after complete atrophy of tail.

of the gill-slits and the absorption of the internal gills. The horny beak is cast off, and the eyes which have hitherto been concealed beneath the skin appear on the surface and are of considerable size. The larva has now become an exclusively air-breathing four-legged adult, which has only to lose its swimming tail in order to acquire its definitive form (Fig. 171).

The duration of tadpole life is usually considerable (some months) and during the later stages the larva breathes by its

lungs as well as by its gills. At the metamorphosis the gill slits close and the animal becomes wholly air-breathing.

The *Amphibia* frequently live in water only during larval life. As terrestrial animals in the adult state they usually choose damp shady places near water, since the cutaneous respiration necessitates a moist atmosphere. The food almost always consists of insects and worms, but in larval life vegetable matters form a considerable part of it. The *Amphibia* can live for months without food, and many of them hibernate buried in the mud, and in hot countries aestivate. They are cold-blooded; and resist a considerable amount of cold, even frost; but if the whole body is frozen they do not recover. The power of regenerating lost parts is considerable, e.g. lost or mutilated limbs. This power is greater in young than in old individuals.

**Distribution.** The *Anura* are almost cosmopolitan. They are represented by one species only (*Liopelma*) in New Zealand and are absent in most Oceanic islands; the latter fact being due to the fatal effect of salt water, especially upon the larvae. The *Urodela* are mainly Nearctic and Palaearctic, and the *Gymnophiona* are confined to the Neotropical, Ethiopian and Oriental regions.

*Urodela* and *Anura* are not found fossil until the Eocene, *Gymnophiona* are unknown in the fossil state.

#### Order 1. GYMNOPTIONA.\* APODA.

*Vermiform Amphibia without limbs or limb-girdles, with biconcave vertebrae, and usually with numerous small scales embedded in the skin. The tail is short or absent, the frontals are distinct from the parietals and the palatines are fused with the maxillaries.*

The body is covered with a smooth, slimy, transversely ringed skin, which contains in the cutis numerous small calcified scales

\* J. Müller, Ueb. d. Kiemenlöcher der jungen Coecilia, *Müller's Arch.* 1835. R. Wiedersheim, Die Anatomie der Gymnophiona, Jena, 1879. G. A. Boulenger, *op. cit.* and *P.Z.S.* 1895, p. 401. P. and F. Sarasin, "Zur Entwick. u. Anat. der *Ichthyophis glutinosus*," *Ergeb. naturwiss. Forsch. auf Ceylon*, 1887. R. Burckhardt, "Hirn u. Geruchsorgan von Triton and Ichthyophis" *Z. f. w. Z.* 52, 1891 p. 370. J. W. Spengel, "Urogenitalsystem der Amphibien" *Semper's Arbeiten*, 3, 1876, p. 1. A. Brauer, Entwick u. Anat. der Gymnophionen, *Zool. Jahrb., Anat.*, 10, 1897, p. 389, and 12, 1899, p. 477.

arranged in transverse rows. The eyes are small, functionless and covered by the skin; though reduced in size, all the usual parts are present. There is on each side of the head behind the external narial opening a small pit which penetrates the maxillary bone and contains a protrusible tentacle-like structure (Fig. 173, T). A well developed harderian gland pours its secretion into this pit. There is no tympanum or tympanic cavity. The anus is close to the hind end of the body, the caudal region being very small or absent. The notochord is persistent (except in the centre of the vertebrae), and the vertebrae are biconcave and numerous, mostly with ribs, which do not meet to form a sternum. The skull (Fig. 173) is compact and has a complete bony roof. The parietals and frontals are separated and there is sometimes a small bone called the turbinal or lateral nasal just external to the outer nostrils (shown, but not marked in Fig. 173). The jugal arch is well developed and joins the parietal and frontal, thus roofing over the temporal fossa; it reaches back to the



FIG. 172.—*Siphonops mexicana* (Règne animal) from Claus.

suspensorium, which appears to consist of fused squamosal and quadrate. The vomer is double and bears teeth. The palatine also bears teeth and extends back on the inner side of the maxilla with which it is continuous. There is a prefrontal, and sometimes a postorbital (postfrontal) which nearly encircles the orbit. The stapes is perforated and is connected with the suspensorium (quadrate). The orbit is small, and the maxilla is perforated by a pit for the tentacular organ. The mandible in some forms has two rows of teeth. The remains of the hyoid and three branchial arches are found in the adult, the hyoid and 1st branchial being connected to the same median piece. The lungs are asymmetrical as in the snakes, the right being much larger than the left which is more or less atrophied.

The conus arteriosus possesses two rows (*Ichthyophis*) or one row (*Siphonops*) of valves, and is without a spiral valve. The ventral aorta is long. There are only two pairs of aortic arches. Of these the first is the systemic (2nd branchial) which gives off the carotid, and the second is the pulmonary. They are joined

by a ductus Botalli. In the larva there is a slender anterior arch (1st branchial), which disappears.

The urinogenital organs are on the usual type (p. 293).

*Gymnophiona* are found in Central and South America, Equatorial Africa, India and the Malay Archipelago. They are not found in the West Indian islands or in Madagascar. They burrow in the surface soil in damp places and near streams. Their eyes which may usually be discerned through the skin are of use only in enabling them to avoid the light. In the male

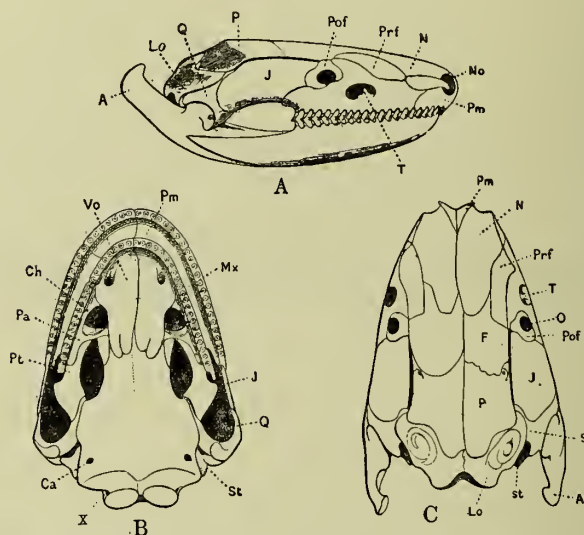


FIG. 173.—Skull of *Ichthyophis glutinosa* (from Gadow, after Sarasin). A from the side; B from below; C from above. A posterior process of the os articulare; Ca carotid foramen; Ch internal narial opening; F frontal; J jugal; Lo exoccipital; Mx maxilla; N nasal; No external narial opening; O orbit; P parietal; Pa palatine; Pm premaxilla; Pof post frontal; Prf prefrontal; Pt pterygoid; Q quadrate; S squamosal; St stapes (columella auris); T tentacular groove; Vo vomer; X foramen for vagus nerve.

the cloacal walls are eversible and when protruded form an intromittent organ by which sperm can be transferred to the cloaca of the female. Fertilisation therefore is internal. Some species, e.g. *Typhlonectes compressicauda*, *Dermophis thomensis*, are viviparous; others are oviparous. The eggs are of considerable size (in *Ichthyophis glutinosa*  $9 \times 6$  mm.) and are meroblastic. In the viviparous forms, so far as is known, the young are born fully developed and there is no larval stage. In the oviparous forms there seems to be some difference in this

respect: in *Ichthyophis glutinosa* (Ceylon) the just hatched young take to the water and lead a larval life of some duration, whereas in *Hypogeophis* (Seychelles) they are hatched ready for a terrestrial life and there is no larval stage.

The development has been examined in two oviparous forms, viz. *Ichthyophis* and *Hypogeophis*, but has not been fully worked out in any species. The eggs are always laid in holes in the ground and the mother remains coiled round them during their development. The segmentation is confined to one pole of the egg, but the layers appear to be formed on the ordinary amphibian type. In *Hypogeophis*, at least, the blastopore persists as the anus. Three external gills of considerable size are developed, but they vanish before hatching. The eggs increase in size and weight considerably during the developmental period owing either to absorption of water or to the supply of nutriment from the cutaneous glands of the mother.

In *Ichthyophis*, in which the breeding season is after the spring monsoon, the eggs become surrounded in the oviduct by a considerable coat of albumen, which becomes twisted in a chalaza-like manner at opposite poles; the embryo moreover acquires a number of cutaneous sense-organs on the head and a lateral line row of similar organs along the body. It also develops a small vertical tail fin and retains a gill-aperture on each side which leads internally to two gill-clefts. The just-hatched larva which is without gills of any kind, either internal or external, makes its way to the nearest water and there lives for a considerable time as an aquatic larva with gill apertures and a tail fin. Eventually these disappear, and the animal takes to its terrestrial burrowing life. The so-called gill apertures being without gills, the larva has to depend entirely upon its lungs for respiration; it frequently rises to the surface to breathe.

In *Hypogeophis*, which appears to breed all the year round, neither lateral line sense-organs nor tail fin are developed, and the gill-clefts are entirely closed at hatching. In this form it has been definitely ascertained that five visceral clefts are formed in the embryo on each side, viz., a small one (spiracle) between the mandibular and hyoid arch, only developed dorsally, and four others, the last being between the third and fourth branchial arches.

The *Gymnophiona* possess a large pronephros which may extend over as many as 12 segments in the larval and embryonic states.

In the present state of our knowledge there can be no question that the *Gymnophiona* must be placed with the *Amphibia*. This is shown by the form of the heart, the presence of a conus arteriosus, the form of the brain and of the urinogenital organs. But they differ from other living *Amphibia* in the form of the skull, the presence of scales in the dermis, the possession of a large meroblastic egg, the absence of a larva breathing by gills, and the absence in the adult of the carotid arch.

There are about 40 living species. The group is not known in the fossil state.



Fam. **Coeciliidae**, with the characters of the order. The genera may be grouped as follows:—

I. Cycloid scales imbedded in the skin.

A. Eyes distinct or concealed under the skin.

1. Two series of teeth in the lower jaw.

a. Jugal (squamosal) and parietal in contact. *Ichthyophis* Fitz., India, Ceylon and Malay Arch.; *Dermophis* Peters, Amer. and Afr.; *Hypogeophis* Peters, E. Afr. and Seychelles; *Coecilia* L., Amer.

b. Jugal separated from parietal. *Rhinatrema* Dum. and Bibr., Amer.; *Geotrypetes* Peters, W. Afr.; *Uracotyphlus* Peters, W. Afr. and India.

2. One series of teeth in lower jaw, *Cryptopsophis* Boul., Seychelles.

B. Eyes below the cranial bones, jugal in contact with parietal. *Hepele* Peters, Panama and Gaboon; *Gymnopsis* Peters, S. Amer.

II. Scales absent.

A. Eyes distinct or concealed beneath the skin.

1. Two series of teeth in the lower jaw. *Typhlonectes* Peters, Amer.; *Chthonerpeton* Peters, Amer.

2. One row of teeth in lower jaw. *Siphonops* Wagl., Amer.; *Bdellophis* Boul., E. Afr.

B. Eyes below the cranial bones.

1. Two rows of teeth in lower jaw, *Gegenophis* Peters. India.

2. One series of teeth in lower jaw, *Scolecormorphus*, E. Afr.

## Order 2. URODELA.\* CAUDATA.

*Scaleless Amphibia with a well developed tail, usually with two pairs of limbs, with or without external gills and gill-slits in the adult.*

The vertebrae are opisthocoelous or amphicoelous even in closely allied forms. The eyes are small, sometimes functionless, and without lids except in the *Salamandridae*. A tympanic membrane and tympanic cavity are not developed. They are usually oviparous, rarely viviparous. Fertilisation is generally internal, sperm transference being effected by application of the swollen lips of the cloacas, or a spermatophore is deposited in the water and sucked up by the cloaca of the female. The sperm is often stored in the seminal receptacles of the female

\* Laurenti, *Synopsis Reptilium emendata* Wien, 1768. Daudin, *Hist. nat. gen. et part. des Reptiles*, Paris 1802-4. Tschudi "Class. der Batrachier," *Mém. Soc. Scien. nat. Neuchâtel*, 2, 1839. Duméril, "Obs. sur la reproduction dans la Ménagerie des Reptiles du Mus. d'hist. nat. des Axolotls," *Nouvelles Arch. du Mus. d'hist. nat. de Paris*, 1860. Boulenger, Gadow, *op. cit.* A. Strauch, "*Revision d. Salamandridengattungen*," Petersburg, 1870. Vaillant, *Mém. pour servir à l'hist. anat. de la Sirène lacertine*, *Ann. Sc. Nat.* (4), 19, 1863.

for a considerable time. The development is almost always partly embryonic and partly larval, but in a few viviparous forms the young are born fully developed. The larva has gills and gill-slits which may or may not persist in the adult. They are mostly aquatic animals, but a few leave the water and are purely terrestrial in the adult state, merely returning to the water to lay their eggs or deposit their larvae. They are carnivorous and live on insects and worms and such like. In a few cases the larvae have the power of developing sexual organs and of reproducing (paedogenesis, neoteny). This frequently happens in the genus *Amblystoma* and occasionally in other genera (*Triton*). They are found all over the temperate parts of the northern hemisphere but do not (*Spelerpes* excepted) extend into the southern. There are about 100 species.

Fam. 1. **Amphiumidae**. Without gills in the adult ; gill-clefts absent or one pair only (between the third and fourth branchial arches) ; with maxillary bones ; both jaws with teeth ; vertebrae amphicoelous ; two pairs of small limbs ; without eyelids ; United States, E. Asia. *Cryptobranchus*\* Leuck., limbs functional with 4 fingers and 5 toes, gill-cleft on both sides or on left side only. *C. (Menopoma) alleghaniensis* Daud., the hellbender, about 18 in., entirely aquatic, E. United States ; *C. japonicus* v.d. Hoev., without gill-openings, in China and Japan 600 to 4500 ft. above sea-level in small streams, may attain to 5 ft., eggs laid in Aug. and Sept. in strings. *Amphiuma* Gard., N. America, gill-opening present, 4 branchial arches, limbs very small, digits 2 or 3 ; *A. means* Gard. to 3 ft., swamps or muddy waters, eggs laid in Aug. and Sept., female coils round them.

Fam. 2. **Salamandridae**.† Without gills or gill slits in the adult, maxillary bones present, both jaws with teeth, with movable eyelids except in *Typhlotriton*, two pairs of limbs.

Sub-fam. 1. **Desmognathinae**. Series of palatal teeth transverse, restricted to posterior portion of vomers, parasphenoid with denticigerous plates, vertebrae opisthocoelous, 5 toes, N. America ; *Desmognathus* Baird, *D. fuscus* Raf., to 5 inches, lungless, eggs in strings wrapped round the body of the female, said to be meroblastic ; *Thorius* Cope, *Th. pennatulus* Cope, under two inches ; *Typhlotriton*, blind, Rock House Cave in Missouri.

Sub-fam. 2. **Plethodontinae**. Like the last except vertebrae amphicoelous and 4 or 5 toes, confined to America except *Spelerpes fuscus*, found in Eur. (mountains near Gulf of Genoa and Sardinia) ; *Spelerpes* Raf., " tongue attached by its central pedicle only, is free all round, ends in a soft knob, and can be shot out to a considerable

\* Hyrtl, *Cryptobranchus japonicus*, Wien, 1865.

† Rusconi, *Amours des Salamandres aquatiques*, Milan, 1821. Id, Hist. nat., development, et metamorphose de la Salamandre terrestre, Paris, 1854. v. Siebold, *Observationes quaedam de Salamandris et Tritonibus*, Berolini 1828. Id. Ueb. d. receptaculum seminis d. weiblichen Urodelen, Z. f. w. Z. 1858.

distance," the young of many species with balancers, 4 fingers, 5 toes free or webbed, limbs well developed except in the worm-like *Sp. parvipes* (Orizaba) and *uniformis* (Costa Rica), several species are lungless, 20 species, N. and C. Amer., N.W. South Amer. (3 species), Hayti (1 species), Eur. (1 species). *Manculus* Cope, N. Amer., with 4 toes, tongue as in preceding; *Anaides* Baird (*Autodax*), tongue cannot be protruded, 5 toes, N. Amer., *A. lugubris* Hallow., entirely terrestrial, lungless, eggs laid in ground and whole development passed through in the egg, embryo with external gills; *Plethodon* Tschudi, N. Amer., tongue as in last, 5 toes; *Batrachoseps* Bonap., tongue as in last, 4 toes, N. Amer.

Sub-fam. 3. **Amblystomatinae.** Series of palatal teeth transverse or posteriorly converging, on posterior portion of vomers; parasphenoid toothless; vertebrae amphicoelous, toes 4 or 5, N. Amer., N. Asia. *Hynobius* Tschudi, 5 toes, Japan; *Salamandrella* Dyb., 4 toes, E. Siberia. *Onychodactylus* Tschudi, fingers (4) and toes (5) with black claws, Japan; *Ranidens* Kessler, 5 toes, E. temp. Asia; *Batrachyperus* Boul., 4 toes, China; *Dicamptodon* Strauch, California; *Amblystoma* Tschudi, palatal teeth in a nearly straight transverse line or an angle, not separated in the middle by a wide interspace, 5 toes, N. and C. Amer., and 1 species (*A. persimile*) in Siam; *A. talpoideum* Holbr. runs in light soils like a mole, S.E. Un. States; *A. tigrinum*, Green, Un. States and Mexico, the larva is the axolotl, which was formerly thought to be an adult form and called *Siredon* (*S. axolotl*, or *S. pisciformis*); the axolotl has a tail fin, 3 pairs of external gills and 4 pairs of open gill clefts, develops sexual organs and lays eggs, it breeds several times a year. The axolotl is found in a state of nature in various parts of Mexico and of the United States. The causes of this retention of the larval characters and the absence of a metamorphosis from an aquatic to a land animal appear to be abundance of food and other favourable conditions of life.\* Larvae bred from axolotls in captivity will in some members of the same brood develop into the *Amblystoma*, in others remain as axolotls. An axolotl, which does not undergo the metamorphosis naturally, may be made † to undergo it by gradually accustoming it to a terrestrial life, but this becomes increasingly difficult as the animal grows older. Axolotls of six months are comparatively easily induced to metamorphose. Further an animal which has become accustomed to a terrestrial life and has partly undergone the metamorphosis may be induced to go back to the larval stage. The axolotl becomes sexually mature at about six months.

Sub-fam. 4. **Salamandrinae.** Palatal teeth in two longitudinal series, diverging behind, inserted on the inner margin of the two palatine processes, parasphenoid toothless, vertebrae opisthocoelous; fingers 4, toes 5 except in *Salamandrina*; mainly Eur., but found in Algeria, E. Asia, Asia Minor, America. *Salamandra* Laur., land-salamanders, tail subcylindrical, Eur., W. Asia; *S. maculosa* Laur., the spotted salamander, eject from the skin glands a poisonous white fluid, viviparous, young are born as larvae from April to June, the eggs then pass into the oviducts and are fertilised before copulation by sper-

\* Gadow, *Nature*, 67, 1903, p. 330.

† V. Chauvin, *Z. f. w. Z.*, 27, 1876, and 41, 1885, p. 365. Velasco, *Biol. Centralblatt* 2, 1882.

matozoa which have been introduced in the previous July and stored until the young of the previous year are born ; *S. atra* Laur. alpine salamander, black, viviparous, produces only two young at a birth,\* which are born fully developed, the uterine young have external gills which absorb nutriment and oxygen, they nourish themselves on other embryos which break down, they are able to live in water if removed before development is completed † ; *S. caucasica* Waja, *Chioglossa* Bocage, Spain, Portugal. *Triton* Laur. (*Molge* Merrem), aquatic salamanders, newts, with laterally compressed tail, Eur., Asia, N. Amer., pair in water, in the pairing the males of some species develop a crest, oviparous, eggs glued singly to stones or water plants, may attain sexual maturity if prevented from metamorphosing (v. Siebold, *Z. f. w. Z.* 28, 1877) ; *T. cristatus* Laur., the crested newt, Gt. Britain, Eur., said to be in rare cases viviparous (Balfour, *Comp. Embryology*, vol. 2), *T. vulgaris* L. (*taeniatus*), Gt. Britain, Eur. *Salamandrina* Fitz. with 4 toes, Italy ; *Tylotriton* Anders., Yunnan, Himalayas ; *Pachytriton* Blgr. China.

Fam. 3. **Proteidae.** Three pairs of external gills and two gill-openings (hyobranchial and last branchial closed) persist throughout life ; maxillaries absent ; premaxillaries, vomer, and mandible toothed, amphicoelous vertebrae, no eyelids, fore and hind limbs present. *Necturus*



FIG. 174.—*Necturus maculatus* (Règne animal) from Claus.

Raf. (*Menobranthus*) 4 fingers, 4 toes, eyes exposed, N. Amer. ; *N. maculatus* (*M. lateralis*) (Fig. 174), 1 foot, spawn Apr. and May ; *Proteus* Laur., the olm, 3 fingers, 2 toes, eyes hidden, Carniola subterranean waters, white turning black if exposed to light, spawn Apr., eggs fastened singly to stones ; *Typhlomolge*, waters of an artesian well in Texas.

Fam. 4. **Sirenidae.** External gills (3 pairs) and gill openings (3 pairs, hyobranchial being closed) through life, maxillaries absent, premaxillaries and mandibles toothless but with horny beaks, amphicoelous vertebrae, no eyelids, hind limbs absent, fore limbs 3 or 4 toes, S.E. Un. States, young larvae unknown, in the youngest known the gills are small and covered by the skin and the respiration is said to be aerial (Cope, *Amer. Nat.* 19, 1885, p. 1226), later the gills increase in size. *Siren* L. 3 gill clefts on each side, 4 fingers, *S. lacertina* Gray, mud-eel, *Pseudobranthus* Gray, 1 gill cleft on each side, 3 fingers.

### Order 3. ANURA.‡ BATRACHIA.

*Scaleless Amphibia without tail, external gills or gill-slits in the adult state ; with four limbs.*

\* Schwalbe, *Zeitsch. Biol.*, (2), 16, 1897, p. 340.

† v. Chauvin *Z. f. w. Z.*, 27, 1876.

‡ Roesel v. Rosenhof "*Historia naturalis ranarum nostratium*," Nürn-



The body is without a tail, and the vertebral column is short, consisting only of nine vertebrae and a urostyle. On the head are the wide mouth and the large eyes, the iris of which has usually a golden lustre. The eyelids are well developed and the lower, which is transparent, can be drawn as a nictitating membrane completely over the eye. The nasal apertures are placed far forward on the extremity of the snout, and can be closed by membranous valves. In the auditory organ there is generally a tympanic cavity, which communicates with the buccal cavity by a short wide eustachian tube and is bounded externally by a large tympanic membrane, which is sometimes free and sometimes concealed beneath the skin. The tongue is absent in the *Aglossa*; it is usually attached between the rami of the lower jaw in such a way that its posterior part is completely free, and can be protruded as a prehensile organ. Ribs are as a rule absent, but the transverse processes of the vertebrae may attain a considerable length. Pectoral and pelvic girdles and limbs are always present. The pelvic girdle is distinguished by the styliform elongation of the ilium. In the skin, which is scaleless, glands with an acrid milky secretion are often aggregated in many places, especially in the region of the ear, where they form large projections (parotoids). Glandular aggregations occur also on the middle divisions of the hind legs (*Bufo calamita*) and on the sides of the body. Reproduction usually takes place in the spring, but Australian frogs spawn when external conditions of moisture allow of it. Sexual congress is confined to an external approximation of the two sexes and almost always takes place in the water. The male, which sometimes has a wart-like elevation on the hand (*Rana*) or gland on the arm (*Pelobates*), embraces the female from the back, usually with the front limbs, and pours out the seminal fluid over the spawn as it issues in strings or in clumps. The individual eggs are surrounded by a viscous layer of albumen which swells up in the water. The larvae have the form of tadpoles.

Some *Batrachia* are purely land animals (toads and tree-frogs),

berg, 1758. Daudin, "*Histoire naturelle des Rainettes, des Grenouilles, et des Crapauds*," Paris 1802. Rusconi, "*Développement de la grenouille commune*," Milan, 1826. C. Bruch, "*Beiträge zur Naturgeschichte u. Classification der nackten Amphibien*," *Würzburger naturg. Zeitschrift*, 1862 and 1863. Boulenger, Ecker, Gadow, *loc. cit.*



which especially love dark and damp hiding places ; others live indifferently on land or in water. In the first case the five toes of the hind feet are entirely without a connecting membrane, or they have an incomplete one ; exceptionally however they are completely webbed (*Pelobates*). In the second case, on the contrary, the hind feet are, as a rule, completely webbed. The land-frogs usually seek the water only at spawning time ; they crawl, run and hop on the land, or dig passages and holes in the earth (*Pelobates*, *Alytes*), or they are able to climb up shrubs and trees by means of discs on the ends of their digits (*Dendrobates*, *Hyla*). About 900 species are known.

Sub-order 1. **AGLOSSA**. There is no tongue and the eustachian tubes are united to open by a median opening into the pharynx. The tympanic membrane is not distinct from the rest of the skin. The vertebrae are opisthocelous and the 2nd, 3rd and 4th carry ribs which tend to fuse with the transverse processes. The transverse processes of the sacrum are dilated and confluent with the urostyle. The epicoracoids do not overlap. The lungs are complex with restricted free lumen. The first spinal nerve is present. They are entirely aquatic in habit. The tadpoles of *Xenopus* have a pair of spiracles (branchial openings), and according to Bles have the normal form but they are without " internal " gills or horny jaws. They feed on micro-organisms and use the gill slits simply for filtering. They possess a sucker, and the external gills are present in the just-hatched form, but soon disappear, the larval respiration being entirely by lungs.



FIG. 175.—*Xenopus (Dactylethra) laevis*.

Fam. 1. **Aglossidae** with the characters of the suborder. *Xenopus* Wagl. (*Dactylethra*), upper jaw toothed, ilia to 9th vertebra, pupil round, phalanges pointed, fingers free, toes broadly webbed and the first three have horny nails, trop. and S. Africa : *X. laevis* the clawed-toad, plathander.

*Hymenochirus*, trop. Afr. *Pipa* Laur., the Surinam toad, tropical Amer., without teeth, fingers free, end in 4 appendages, skin papillated, the eggs which are laid after the rains appear to be fertilised internally and placed by the protruded cloaca upon the back of the female where they sink into the skin (Bartlett, *P.Z.S.* 1896, p. 595), each egg-containing pouch in the skin so formed is covered by a lid the origin of which is unknown; the young leave these skin cells in a condition closely resembling the adult, the tail formed in the embryo being absorbed before hatching.

Sub-order 2. **PHANEROGLOSSA.** A tongue is present and the eustachian tubes are separate. The tadpoles have one spiraculum only, on the left side except in the *Discoglossidae* in which it is median.

Series A. **ARCIFERA.** The epicoracoids of the two sides overlap.

Fam. 2. **Discoglossidae.** Upper jaw toothed, transverse processes of sacral vertebra dilated, short ribs to anterior transverse processes, vertebrae opisthocelous, tongue a round non-protrusible disc, males without vocal sacs, tadpoles with median spiracle. *Discoglossus* Otth, S. Eur., N.W. Afr., tympanum indistinct. *Bombinator* Merr., Eur., Asia, no tympanum; *B. igneus* Günth, unke, fire-bellied toad. *Alytes* Wagl., tympanum distinct, the male attaches the eggs to its hind limbs, where they remain until hatching, Eur.; *A. obstetricans* Laur. *Liopelma* Steindachn., New Zealand, no tympanum or eustachian tubes, the only New Zealand Amphibian.

Fam. 2. **Pelobatidae.** Upper jaw toothed, transverse processes of sacral vertebra dilated, no ribs; tongue protrusible, vertebrae procoelous except in *Asterophrys* and *Megalophrys* where they are opisthocelous; tympanum hidden or indistinct, absent in *Pelobates*. *Scaphiopus*, spade-foot, N. Amer., Mexico. *Pelobates* Wagl. spade-footed toad, Eur., inner tarsal tubercle shovel-shaped; *P. fuscus* Laur., Central Eur., 3 inches, tadpole larger than adult. *Pelodytes* Fitz., S.W. Eur., *Batrachopsis* Blgr., New Guinea; *Leptobrachium* Tschudi, E. Ind.; *Xenophrys* Günth, mountains of India; *Megalophrys* Kuhl, E. Ind.; *Asterophrys* Tschudi, New Guinea; *Ranaster* Mackay, N. Guinea.

Fam. 2. **Bufonidae.** Toads. Teeth absent, except in *Notaden* which has them on the vomers; transverse processes of sacral vertebra dilated; tympanum usually distinct, but variable; vertebrae procoelous, without ribs; includes terrestrial, burrowing, aquatic (*Nectes*) and probably arboreal (*Nectophryne*) forms; nearly cosmopolitan, absent from Madagascar, Papuasias and Pacific Islands, and New Zealand. *Engystomops* Espada, trop. Amer.; *Pseudophryne* Fitz, Australia; *Nectophryne* Buchh. and Peters, W. Afr., E. Ind.; *Bufo* Laur., pupil horizontal, metasternum cartilaginous, sometimes ossified along the middle; fingers free; toes more or less webbed, tips simple or dilated into small discs, more than 100 species, cosmopolitan except Australian region and Madagascar; *B. vulgaris* Laur., common toad of the palaearctic region, is absent from Ireland, male without vocal sacs, in S. Eur. may attain to 6 inches, devour insects, worms, snails, and have been known to eat mice; skin is dry but can exude a white poison, harmless and useful creatures; *B. calamita* Laur., the natterjack, W. Eur., England, Wales and S.W. Ireland. *Nectes* Cope, Java; *Notaden* Günth., Australia; *Myobatrachus*

Schleg., Aust.; *Rhinophrynus* Dum. and Bibr., Mexico. *Codophryne*, Himalayas.

Fam. 4. **Hylidae**. Tree-frogs. Upper jaw toothed (*Amphignathodon* Blgr. of Ecuador possesses teeth in the lower jaw also), transverse processes of sacral vertebra dilated, terminal phalanges claw-shaped and swollen at the base and carry an adhesive cushion; vertebrae procoelous, no ribs; tympanum free or hidden; with the exception of *Hyla arborea* and two other species found in N. India and S. China are exclusively American or Australian (absent from Madagascar and Africa). *Thoropa* Cope, Brazil; *Chlorophilus* Baird, N. Amer., Peru, includes the smallest frogs, less than  $\frac{3}{4}$  in.; *Acris* Dum. and Bibr. N. Amer.; *Hyla* Laur., pupil horizontal, tympanum distinct or hidden, fingers and toes with adhesive discs, more than 150 species, cosmopolitan except ethiopian region; *H. arborea* L. the tree-frog of Europe; *H. faber* Wied., the ferreiro or smith, the female makes pools with mud walls for the eggs (*P.Z.S.* 1895, p. 89), Brazil; *H. goeldii*, eggs carried on back of female, Brazil. *Nototrema* Günth. (*Notodelphys* Weinl.), female has a pouch on the back opening behind for reception of eggs, some at least emit tadpoles, trop. Amer. *Hylella* Reinh. and Lüttk. trop. Amer. and Australia. *Nyctimantis* Blgr., Ecuador. *Agalychnis* Blgr., C. Amer. *Phyllomedusa* Wagl., lays its eggs on leaves of plants overhanging water into which the tadpole falls at hatching (*Budgett, Q.J.M.S.* 42, 1899, p. 313), trop. Amer. *Triprion* Cope, Yucatan; *Diadlena*, *Corythomantis*, *Pternohyla*.

Fam. 5. **Cystignathidae**. Upper jaw toothed, transverse processes of sacral vertebra not or but slightly dilated, terminal phalanges never claw-shaped; auditory organ variable; a large family exhibiting great variety of habit (aquatic, terrestrial, arboreal, burrowing) and presenting alliances to other families, mostly neotropical, but found also in trop. C. Amer., and in Australia and Tasmania.

Sub-fam. 1. **Hemiphractinae**. Teeth in both jaws, vertebrae opisthocelous, tympanum distinct, S. Amer. *Hemiphractus* Wagl., Ecuador and Colombia; *Ceratohyla* Espada, Ecuador; *Amphodus* Ptrs., Brazil.

Sub-fam. 2. **Cystignathinae**. Teeth in upper jaw only, vertebrae procoelous. *Pseudis* Laur., with teeth in upper jaw only, fingers free, toes webbed, pupil horizontal, first finger opposite the others, S. Amer.; *Ps. paradoxa* L.  $2\frac{1}{2}$  inches, with enormous tadpole to 10 inches, Guianas; *Hylodes* Fitz., trop. Amer.; *H. martinicensis* Tschudi, large eggs, embryo without gills or clefts hatched as perfect frog, W. Indies; *Calyptocephalus* Bibr., dermal ossification of cranium, large tadpoles, Chili, Panama; *Ceratophrys* Boie, horned toads, toad-like, some species with a bony dorsal shield in the cutis, eyelid often as an upright triangular appendage, S. Amer.; *Lepidobatrachus* Budgett, Paraguay; *Leptodactylus* Fitz., fingers and toes not webbed, trop. Amer.; *Paludicola* Wagl., trop. and S. Amer.; *Centrolene* Espada, Ecuador; *Cyclorhamphus* Tschudi, Brazil; *Telmatobius* Wiegman, W. S. Amer.; *Elosia* Tschudi, Brazil; *Edalorhina* Esp., Ecuador and Peru; *Plectromantis* Ptrs., W. S. Amer.; *Limnomedusa* Cope, Uruguay; *Hylorhina* Bell, Chili; *Borborocoetes* Bell, W. S. Amer.; *Zachaeus* Cope, Brazil; *Hypopsis*, S. Amer.; *Chiroleptes* Gthr., first finger opposed to the others, Australia; *Heleioporus* Gray, Australia; *Limnodynastes* Fitz., Australia; *Crinia* Tschudi, Australia; *Mixophyes* Gthr., Australia; *Cryptotis* Gthr., Australia; *Hyperolia* Cope, Australia.

Sub-fam. 3. **Dendrophryniscinae**. Without teeth. *Batrachophrynus* Ptrs., an aquatic genus without tympanum and eustachian tubes, Peru; *Dendrophryniscus* Esp., Brazil.

Series B. FIRMISTERIA. The epicoracoids do not overlap but are firmly united with one another.

Fam. 6. **Engystomatidae**. Transverse processes of sacral vertebra dilated, vertebrae procoelous and without ribs; the precoracoid may be weak or absent.

Sub-fam. 1. **Engystomatinae**. Without teeth in the upper jaw; neotropical and palaetropical; many genera live on ants; the mouth is often small and the snout projecting; in some genera the digits have adhesive discs supported by T-shaped phalanges. The sub-family includes terrestrial, aquatic and burrowing forms but none are arboreal. *Rhinoderma* Dum. and Bibr., Chili, *Rh. darwini* D. and B., total length 3 cm., male with a subgular vocal sac to which the eggs are transferred and in which they develop, the tadpoles are without gills and the whole development appears to take place in the pouch; *Phryniscus* Wieg., trop. Amer.; *Brachycephalus* Fitz., with broad dorsal osseous shield, S. Amer.; *Stercocyclops* Cope, Brazil; *Engystoma* Fitz., Amer.; *Oreophrynella*; *Hypopachus* Keferst., trop. Amer.; *Melanobatrachus* Beddome, India; *Sphenophryne* Ptrs. and Doria, New Guinea; *Liophryne*, New Guinea; *Calophrynus* Tschudi, E. Indies, S. China; *Microhyla* Tschudi, China, E. Indies; *Callula* Gthr., E. Indies; *Xenobatrachus* Ptrs. and D., New Guinea; *Phrynomantis* Ptrs., Africa and Amboina; *Cacopus* Gthr., India; *Glyphoglossus* Gthr., India; *Breviceps* Merr., Africa; *Hemisus* Gthr., Africa; *Rhombophryne* Boettg., Madagascar; *Scaphiophryne* Blgr., Madagascar; *Xenorhina*, Ptrs., New Guinea; *Phrynella*, Malacca; *Manophryne*, New Guinea; *Cacosternum*, Africa.

Sub-fam. 2. **Dyscophinae**.\* With teeth in the upper jaw; those with disced digits are climbers. *Calluella*, Burmah, all the other genera from Madagascar, viz. *Dyscophus*, *Plcthodontohyla*, *Mantipus*, *Platyhyla*, *Phrynocara*, *Platypelis*, *Cophyla*, *Anodontohyla*.

Sub-fam. 3. **Genyophryinae**. With very small teeth on the anterior portion of the lower jaw. *Genyophryne*, Sudest Island between N. Guinea and the Louisiade Archipelago.

Fam. 7. **Ranidae**. Transverse processes of sacral vertebra cylindrical; the precoracoids are always present; vertebrae procoelous.

Sub-fam. 1. **Ceratobatrachinae**. Teeth in both jaws; tongue notched and free behind; pupil horizontal; tympanum distinct; fingers and toes free, with swollen tips; male with two internal vocal sacs. *Ceratobatrachus*, Solomon Islands.

Sub-fam. 2. **Raninae**. With teeth in the upper but none in the lower jaw; tympanum variable; adhesive discs present or absent; tongue free behind, sometimes notched; terrestrial, arboreal and aquatic forms are known; mainly aretogaean, 3 species in Papuan region and 4 genera in the tropical andesian. *Phylllobates* D. and B., trop. Amer.; *Oryglossus* Tsch., E. Indies; *Rana* L., frogs, pupil horizontal, vomers with teeth, fingers free, toes webbed, 4th and 5th metatarsals diverging and webbed together, cosmopolitan except the S. parts of S. Amer. and New Zealand, one species in N. Australia; *R. temporaria* L., the common European brown or grass-frog, spawn

\* Boulenger, *Ann. and Mag. Nat. Hist.* (6), 4, 1889, p. 247.



end of Febr. or beginning of March, hatch in about 5 days, leave the water in about 3 months, Eur., N. and temp. Asia; *R. esculenta* L., the common water-frog of Europe, also in W. Asia and N.W. Africa, is found locally in England at Foulmire Fen and Thetford etc., probably introduced; *R. silvatica* Leconte, N. Amer.; *R. catesbiana* Shaw (*muigiens*), bull-frog, E. N. Amer., to 7 in., will take ducklings; *R. opisthodon*, Solomon Islands, the whole metamorphosis takes place in the egg. *Rhacophorus* Kuhl, E. Indies, Japan, Madagascar, many species have dermal appendages, in *Rh. pardalis* (Borneo, Phillipines) the webbed hands and feet are much enlarged and act as parachutes; the female of *Rh. reticulatus* of Ceylon attaches the eggs to the surface of her belly, in other species the eggs are laid out of water in a foamy mass. *Chiromantis* Ptrs., trop. Afr. *Ixalus* D. and B., E. Indies. *Micrixalus*, India. *Chirixalus*, Karin Hills. *Cornufer* Tsch., Polynesia, Austro-Malayasia, Phillipines. *Phrynobatrachus* Gthr., Africa. *Nyctibatrachus* Blgr., India. *Nannobatrachus* Blgr., Ind. and Ceylon. *Nannophrys* Gthr., Ceylon. *Arthroleptis* Smith, Africa, Madagascar, islands of Indian Ocean, in *A. seychellensis* the tadpoles are sometimes found adherent to the back of the adult. *Rappia* Gthr., trop. Afr. and Madagascar. *Megalixalus* Gthr., trop. Afr. and Madagascar. *Cassina* Gir., trop. Afr. *Hylambates* A. Dum., trop. Afr. *Hylixalus* Esp., Ecuador. *Prostherapis* Cope, S. Amer. *Phyllodromus* Esp., Ecuador. *Colostethus* Cope, Colombia. *Trichobatrachus* Blgr., Congo; *Gampsosteonyx* Blgr. Congo; *Phrynopsis*, Mozambique; *Batrachylodes*, Solomon Islands; *Phrynoderma*, Karin Hills; *Oreobatrachus*, Borneo.

Sub-fam. 3. **Dendrobatinae**. Teeth absent. *Mantella* Blgr., Madagascar; *Dendrobates* Wagl., trop. Amer., *D. tinctorius* strongly poisonous cutaneous secretion, *D. braccatus* of Brazil carries its tadpoles on its back. *Cardioglossa*, the Gaboon.

#### Order 4. STEGOCEPHALI.\*

The *Stegocephali* are extinct salamander-like or lizard-like Amphibia in which the dorsal surface of the skull is completely covered by dermal bones. There is also usually a greater or less development of bony dermal plates on other parts of the body, and a parietal foramen is present between the parietal bones. They make their appearance in the Lower Carboniferous and extend through the Permian into the Upper Trias in which they disappear. They are the earliest known pentadactyle animals.

The vertebral column varies considerably in structure. In some forms the notochord appears to have been persistent and almost unconstricted, while at the other extreme of modification solid slightly amphicoelous vertebrae are present (Labyrinthodonts). The ribs, which are one- or

\* Sometimes termed *Phractamphibia*. For literature and fuller account see Zittel, *Grundzüge der Paläontologie*, 1895 (English edition, Macmillan & Co., 1902); and Woodward, *Vertebrate Palaeontology*, 1898.



two-headed are short and never completely encircle the thorax so as to reach any sternal elements. The skull is in many respects amphibian-like but in some features it recalls the *Reptilia*. It is always covered by a number of bony plates which appear to have been dermal in position and recall in many respects the condition found in ganoid fishes and in crocodiles. In many forms the occipital region of the cartilaginous cranium appears to have been unossified, and there is a ring of small sclerotic plates round the eye. In some of the palaeozoic genera (*Branchiosaurus* etc.) unmistakable remains of bony branchial arches are present. The teeth are conical; they are usually present on the jaws and sometimes on the palatines and vomers. In the Labyrinthodonts the pulp-cavity gives off branching diverticula into the dentine and the surface of the dentine is folded in a complicated manner as in certain extinct crossopterygian fishes. The shoulder girdle, though imperfectly

known appears to have had scapula (cleithrum), clavicle, coracoid and interclavicles. The limbs are on the normal pentadactyle type and present no approximation to those of fishes. The hand when known presents 4 digits, the foot 5.

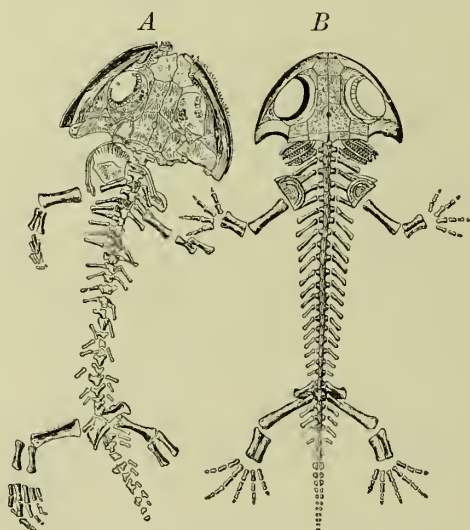


FIG. 176.—*Branchiosaurus amblystomus* Credner. A skeleton of adult (nat. size). B restoration of a larva with branchial arches (after Credner, from Zittel).

The *Stegocephali* appear to have been fresh-water or terrestrial animals. Although generally referred to the *Amphibia*, their systematic position cannot be regarded as fixed. The reason

for regarding them as *Amphibia* is the presence of gill-arches in some genera, the fact that the ribs never so far as is known reach a sternum and that traces of the lateral line system of sense-organs are suggested by grooves on some of the cephalic scales. But it must be remembered that these and other features often asserted as characteristic of the *Stegocephali* have only been found in some forms; and that some members of the group possess features which suggest reptilian affinities. We shall probably not be far wrong in assuming that the order as at present constituted is a composite one, containing genera some

of which are amphibian and others reptilian. But whatever view be taken on this point, it is clear that none of them can be regarded as bridging the gulf between the piscine and terrestrial type, for not only do they all present fairly specialised skeletal features, but in all in which the extremities are known the pentadactyle type of skeleton is fully developed.

Sub-order 1. **BRANCHIOSAURI.** Small salamander-like animals, with well developed gill arches in what are supposed to be immature specimens. Occipital region of skull unossified. Carpus and tarsus cartilaginous. Ventral scales thin and in rows. Upper Carboniferous and Permian. *Branchiosaurus* Fritsch (*Protriton*, *Pleuronura*), Lower Permian of Saxony, Bohemia and France (Fig. 176); *Pelosaurus* Credner; *Melanerpeton* Fritsch; *Dawsonia* Fritsch; *Amphibamus* Cope; *Pelion* Wyman; *Urocordylus* Huxley and Wright.

Sub-order 2. **AISTOPODA.** Body long, snake-like without limbs or pectoral girdle; vertebrae amphicoelous. Upper Carboniferous, Lower Permian. *Dolichosoma* Huxley, *Ophiderpeton* Huxley.

Sub-order 3. **LABYRINTHODONTIA.** The dentine of the teeth is much folded, ventral armour is usually present. From the Lower Carboniferous to the Trias. *Archegosaurus* H. v. Meyer, with ventral armour, 4 fingers, 5 toes, Lower Permian; *Sparagmites* Fritsch; *Chelidosaurus* Fritsch; *Actinodon* Gaudry, etc. *Mastodonsaurus* Jaeger, the largest Labyrinthodont, the skull may attain a length of 1.25 m., Trias; *Trimatosaurus* Braun; *Labyrinthodon* Owen, Keuper. Labyrinthodonts are described from the Trias of S. Africa and of New South Wales. Footprints which are supposed to have been made by Labyrinthodonts are found in the Lower and New Red Sandstone of Europe, Africa and America. Such footprints usually show five fingers and five toes, which is inconsistent with this view as no Labyrinthodont is known to have 5 fingers.

The MICROSAURIA from the Upper Carboniferous and Lower Permian with *Hyloplesion*, *Petrobates*, *Keraterpeton*, *Lepterpeton*, *Seeleya* etc., are usually placed with the Stegocephali.

## CHAPTER XI.

### CLASS REPTILIA.\*

*Cold-blooded, usually scaly Vertebrata, with a right and a left aortic arch, a single occipital condyle, and pulmonary respiration. The ovum is large and meroblastic, and the embryo has an amnion and allantois.*

The class Reptilia is represented at the present day by lizards, snakes, turtles, tortoises, crocodiles, and the New-Zealand lizard, *Sphenodon*. These however are but a very small proportion of the whole class. The extinct groups, which are almost confined to the secondary period of geological history, form by far the most important part of the class both in variety of structure and habit, and in strangeness of form. Of the living groups the lizards and snakes are almost entirely terrestrial, and not found fossil earlier than the tertiary period and then only in small numbers; the *Chelonia* and *Crocodylia*, which are partly aquatic, date from the beginning of the secondary period, while *Sphenodon* is the representative of a sub-order which made its appearance in the Permian and has persisted to the present day.

Among the extinct forms we find the whale-like marine *Ichthyosauria*, the bird-like flying *Pterosauria*, the huge bipedal *Dinosauria*, and the mammal-like *Anomodontia*. It is a significant fact that some of the most highly specialized and ancient of the Reptilia, such as the *Chelonia* and *Pterosauria*, make their first appearance with all their special characters fully developed; and in none of the eight sub-classes can it be said that the earliest forms are definitely annectant to other sub-classes.

\* For literature of living forms see the subclasses. For extinct forms see Zittel, *Grundzüge der Palaeontologie*, Leipzig, 1895, and the same translated into English, 1902, Macmillan & Co., London. A. S. Woodward, *Vertebrate Palaeontology*, Cambridge, 1898. For general account of Reptiles see H. Gadow, *Amphibia and Reptiles* (Cambridge Natural History), Macmillan & Co., 1901; and C. K. Hoffmann, *Reptilien*. in Bronn's Klassen u. Ordnungen des Thierreichs.

The *Reptilia* are essentially scaly tetrapódous, pentadactyle animals, but great modification in form and habit are met with in the group. Functional gills are not developed at any time of life, and they usually lay large yolked eggs which develop outside the body of the mother.

The integument is scaly in all living reptiles. The scales are horny epidermal structures usually placed on dermal papillae. In some cases (*Chelonia*, some *Crocodylia*, and *Lacertilia*), osteoderms may be present in the cutis in some parts of the body. It is possible that in some of the extinct forms e.g. *Ichthyosauria*, scales may have been absent.

An upper and lower eyelid is generally present, and frequently a third eyelid, the nictitating membrane. A tympanic membrane is also usually present. But in snakes there is no tympanic membrane, and the eyelids are transparent and fused over the eye, so that they appear to be absent.\* There is a cloaca which receives the openings of the urinogenital ducts, and opens to the exterior by the anus. The tail is usually of considerable length, and the limbs are sometimes capable of supporting the weight of the body; but more often they serve merely to push on the body which glides along the ground on its belly. In snakes and some lizards limbs are absent.

Cutaneous glands are confined to certain places and are not generally distributed. The skin is usually diversely coloured, owing to the presence of pigment in the dermis and sometimes in the deeper layers of the epidermis.

The phenomenon of colour-change is met with in lizards and some snakes: it is particularly developed in the chameleons.

The endoskeleton is well ossified, and the membrane bones are so closely incorporated with the skeleton that they cannot be peeled off.

The vertebral column is usually divided into cervical, thoracic, sacral and caudal regions. The faces of the centra vary considerably: they are frequently hollow in front and convex behind (procoelous), but they may be flat, or hollow at both ends (amphicoelous), or even hollow behind (opisthocoelous). The amphicoelous condition is found in some extinct forms and in *Sphenodon* and the *Geckonidæ* among the living. In this case

\* It is possible that they are absent and that the transparent membrane stretched across the eye is the nictitating membrane.

remains of the notochord occupy the intercentral spaces. The neuro-central suture persists in many forms and it is common to find separate cervical ribs. The cervical ribs are usually double-headed, but the ribs of the thorax may be single or double-headed. A lumbar region in which the ribs are indistinguishable in the adult is usually present. In *Sphenodon* and crocodiles the vertebral part of the ribs carry a posteriorly-directed process, the *uncinate* process. The sacrum in living forms, if present, nearly always consists of two vertebrae, but is often more extensive in the extinct groups. It is absent in *Ophidia*, *Mosasauria* and *Ichthyosauria*. Chevron bones (haemal arches) are frequently present in the caudal region, and are usually attached between the centra. Wedge-shaped intercentral bones are sometimes found between the vertebrae of the cervical and caudal regions.

A sternum is very generally present (absent in *Ophidia* and *Chelonina*). It is rhomboidal, and may be cartilaginous. The ribs which reach it belong to the anterior part of the thoracic region of the vertebral column, and the hindermost of them are generally attached to a single or double backward prolongation of it. Abdominal ribs are splint-like membrane bones placed in the ventral abdominal wall of *Sphenodon*, crocodiles, and some extinct groups. They are of the nature of osteoderms and have nothing to do with true ribs.

In the skull there is a single occipital condyle (*Monocondylea*), to which the exoccipitals usually contribute. In the auditory region three bones are developed, the epiotic, opisthotic and prootic. Of these it is characteristic that the epiotic unites with the supra-occipital, and the opisthotic with the exoccipital, before either of them unites with the prootic or with each other. The prootic usually remains distinct.

The basisphenoid bone is always present, and sometimes the alisphenoid, but the presphenoid and orbito-sphenoid are usually absent. The presphenoid is frequently replaced by a splint (basisphenoidal rostrum) formed of membrane bone and projecting forwards from the basisphenoid. This splint represents the anterior part of the parasphenoid of the Ichthyopsida, and remnants of the posterior part of the same bone are sometimes present on the ventral side of and fused to the basisphenoid. The alisphenoid and orbito-sphenoids are likewise sometimes



replaced by downwardly projecting processes of the parietals and frontals, or by a bone known as the epipterygoid (columella cranii). The parietals and frontals are paired or unpaired and there is a squamosal which is usually attached to the parietals. The quadrates which are always present and give articulation to the lower jaw are moveably (*Streptostylica*) or immoveably (*Monimostylica*) attached to the skull. They are usually carried by outwardly projecting processes (*parotic* processes) of the auditory region into which the prootic, opisthotic and exoccipital bones enter ; but they are also attached to the squamosals, which may in some extinct forms overlap them externally so much as almost to conceal them. This condition is an approximation to that of mammals in which the quadrate must be regarded as being indistinguishably fused with the squamosal. The nasal capsules remain largely cartilaginous and are covered dorsally by the premaxillae, nasals and prefrontals. There is always a prefrontal and a postfrontal, and usually a lacrymal. The orbit is generally completed behind by the union of the postfrontal with the jugals, between which a separate bone, the *postorbital*, may be intercalated. The temporal fossa, which is thus cut off from the orbit, is frequently divided into two by a bridge of bone formed by the postfrontal sending backwards a process to unite with an anteriorly directed process of the squamosal. This bridge is called the supratemporal arcade and the cavity between it and the skull the supratemporal fossa or vacuity. Moreover the jugal is in many forms connected with the lower end of the quadrate by a quadrato-jugal, which constitutes the infratemporal arcade and forms the lower boundary of what may be called the lateral temporal fossa or vacuity. In *Rhynchocephalia*, *Dinosauria*, *Crocodylia* and *Pterosauria*, both these arcades and both fossae are present ; in *Ichthyosauria*, *Plesiosauria*, and *Anomodontia*, both arcades appear to be present, but they are continuous and the lateral temporal fossa is absent or very small (in some *Anomodontia*), so that there is only one broad temporal arcade and one fossa (the supratemporal). In *Chelonia* there is, as a rule, only one arcade, but it consists of jugal and quadrato-jugal only and is the lower one, the supratemporal arcade not being developed (this is the mammalian arrangement, save for the presence of a quadrato-jugal). In the *Lacer-*

*tilia* the supratemporal arcade alone is present and in *Ophidia* both arcades are absent.

In many reptiles, e.g. *Rhynchocephalia*, *Crocodilia*, *Lacertilia* and some *Chelonia* the parietal sends out a process which reaches the squamosal: this is the parieto-squamosal or posterior temporal arcade, which forms the superior boundary of a posterior temporal fossa, the lower boundary of which is formed by the parotic process of the exoccipital and periotic bones.

The palate varies considerably in structure in the different groups, but the pterygoids tend to converge rapidly towards the middle line, instead of being parallel or even divergent as in the Amphibia.\* The palatal vacuities may be extensive as in *Lacertilia* and *Ophidia*, or there may be a continuous bony palate with secondary palatal plates, as in *Chelonia* and *Crocodilia*. A transpalatine (ectopterygoid) connecting the pterygoid and maxilla is present in many forms.

The lower jaw is composed of five membrane bones, the dentary, splenial, angular, surangular and coronoid, and of a cartilage bone the articular. Meckel's cartilage often persists through life.

In the shoulder girdle there is a scapula and a coracoid which reaches the sternum, when that structure is present; and clavicles and interclavicles are frequently found. The humerus is provided with one or two condylar foramina in *Sphenodon* and some extinct forms, and the number of digits varies from two to five, or in *Ichthyosauria* to even a larger number.

The pelvis exhibits great variations which are described later under the orders: it may even be mammal-like (some *Anomodontia*) or bird-like (*Dinosauria*). The ankle-joint is intertarsal and the number and form of the toes vary considerably.

**Central nervous system.**—The spinal cord possesses except in snakes cervical and lumbar enlargements and in some extinct forms the lumbar swelling seems to have been larger than the brain.

The cerebro-spinal axis is bent at the junction of spinal cord and brain. The cerebral hemispheres (Fig. 177) are small and smooth; they are largest in the *Crocodilia*. There are two optic lobes. The cerebellum is a mere strip in snakes and lizards: it is rather larger in *Chelonia*, and in *Crocodilia* it consists of a

\* Mr. Lister has called my attention to this character, which has not, so far as I know, been noticed before.

central vermis and two small lateral lobes. There is a parietal organ in *Sphenodon* (Fig. 178) and Lacertilia, which is described below under Lacertilia. There are twelve pairs of cranial nerves except in snakes in which the spinal accessory is absent. The facial is not united with the trigeminal, and the glosso-pharyngeal is an independent nerve though it has several connections with the vagus. The hypoglossal or twelfth cranial nerve passes out through a foramen or sometimes more than one foramen in the exoccipital bone. The 9th, 10th, and 11th nerves leave the skull together.

The 3rd nerve gives off a twig to the muscle of the upper eyelid. The 6th supplies the muscles of the nictitating membrane and the retractor bulbi. The 5th nerve has two roots, a smaller motor and a larger sensory. The ophthalmic nerve which sometimes has a special ganglion corresponds to the R. ophthalmicus superficialis portio trigemini of fishes. The 7th has become mainly a motor nerve; it gives off a palatine nerve, which may anastomose with the superior maxillary, and a mandibular branch which enters into similar relations with the inferior maxillary. The main nerve passes back dorsal to the columella auris and supplies the muscles of the hyoid, the cutaneous muscles of the neck, and the mylohyoid. The 7th nerve sends off anastomosing branches to the 9th (Jacobson's anastomosis). The 10th nerve possesses a ganglion of the trunk as well as of the root.

The spinal accessory is a part of the vagus which becomes distinct in *Sauropsida* and *Mammalia*. It arises by several roots from the spinal cord between the dorsal and ventral spinal nerve-roots as far back as the third spinal nerve, and passes forwards through the foramen magnum into the skull which it leaves in association with the vagus. It supplies the trapezius and other muscles. Part of its fibres enter the vagus.

The hypoglossal may be regarded as being generally homologous with the spino-occipital nerves (ventral vagus roots) of fishes. It represents a variable number of anterior spinal nerves which have lost their dorsal roots and become associated to form an additional cranial nerve.

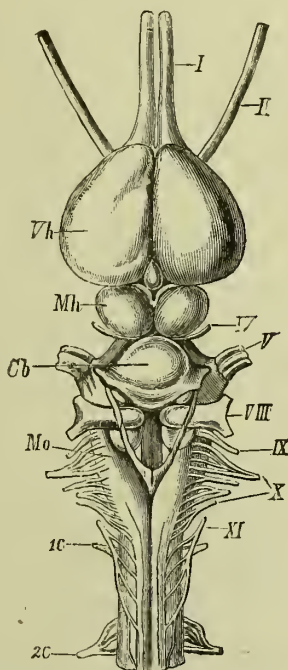


FIG. 177.—Brain of the Alligator, dorsal view (after Rabi Rückhard), *Cb* cerebellum; *Mh* optic lobes (corpora bigemina); *Mo* medulla oblongata; *I* olfactory lobes; *II* optic, *IV* trochlear, *V* trigeminal, *VIII* auditory, *IX* glossopharyngeal, *X* vagus, *XI* spinal accessory nerves; *1C*, *2C* first and second spinal nerves; *Vh* cerebellum.

The **sympathetic** system consists typically of a chain of ganglia on each side commencing at the upper end of the neck and extending the whole length of the trunk and possibly into the tail (caudal canal). Its anterior end enters the skull and connects with some of the cranial nerves. In crocodiles the cervical sympathetic is double as in salamanders: a deep portion lies in the vertebral-arterial canal of the ribs, and a superficial in the usual position; both are connected with the spinal nerves and with each other by rami communicantes.

The **eyes** are always present though they vary considerably in size. The sclerotic is provided with a circle of bony plates in *Chelonia* and *Lacertilia*. A vascular pigmented fold very

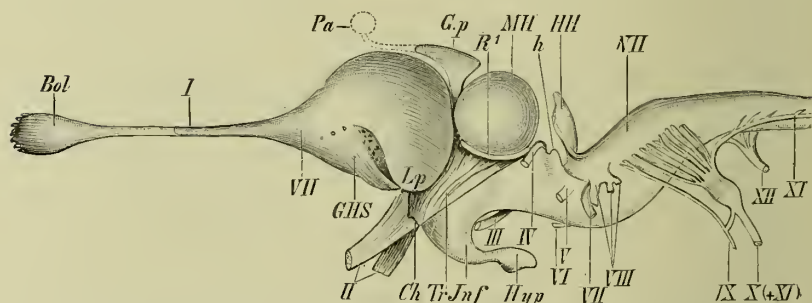


FIG. 178.—Brain of *Sphenodon*. Side view (after Wiedersheim). *BoL* swollen termination of olfactory lobe; *Ch* optic chiasma; *GHS* pedunculi cerebri; *G.p* pineal body; *HH* cerebellum; *Hyp* pituitary body; *h* small prominence in front of the cerebellum; *Jnf* infundibulum; *Lp* lateral projection of cerebellum; *MH* optic lobes; *NH* medulla oblongata; *Pa* parietal organ; *Tr* tractus nervi optici; *VH* cerebrum; I–XII the twelve cranial nerves.

similar to the pecten of birds projects into the vitreous humour in most *Lacertilia* and in *Crocodylia*. A retractor bulbi is present except in *Ophidia*. There is usually an upper and lower eyelid and a nictitating membrane, but in *Ophidia*, *Amphisbaenidae* and geckos eyelids appear to be absent (p. 317). There are two lacrymal glands,—the *harderian* (gland of the nictitating membrane) on the inner (anterior) side of the eyeball, and the lacrymal on the outer (posterior) side.

**Auditory organ.** The membranous labyrinth as in most *Pisces* and *Amphibia* is divided into a pars superior or *utricle* with its three semicircular canals, and a pars inferior or *sacculle* which gives off posteriorly and ventrally a cochlear process (sometimes called *lagena*). The cochlear process is tubular in



crocodiles and *Sphenodon*, and slightly bent, thus resembling that in birds and foreshadowing the spiral cochlea of mammals. In many reptiles the ductus endolymphaticus (aqueductus vestibuli) ends in the cranial cavity just beneath the skull roof, and in the *Ascalabota* it extends from the skull cavity into the neck, swelling into a large lobed sack in the neighbourhood of the shoulder girdle. It is filled with a soft otolithic mass.

The patches of sensory epithelium in the membranous labyrinth, where the branches of the auditory nerves end, are as follows : (1) in each ampulla there is a projection of sensory epithelium known as the *crista acustica* ; (2) there is a patch in the sacculæ and utricle known as the *macula acustica* of the sacculæ and utricle respectively ; (3) on the floor of the utricle there is an additional patch, the *macula acustica neglecta* ; (4) in the cochlear there are two patches, the *papilla acustica basilaris* and the *papilla acustica lagenae*. In the *Chelonia* and *Ophidia* the cochlear process is hardly differentiated into a *pars basilaris* next the utricle and a peripheral lagena, but in the *Crocodylia* the *pars basilaris* is well developed and forms the main part of the ductus cochlearis, the lagena being merely a terminal end-sac. The *papilla acustica basilaris* which is contained in the *pars basilaris* is not differentiated into the organ of Corti, but in crocodiles the membrane on which it is placed is called the *membrana basilaris* and there is an indication of the *scala vestibuli*, *scala tympani* and membrane of Reissner.\*

A tympanic cavity, membrane and eustachian tube are present except in snakes and apodal lizards. There is a fenestra rotunda as well as a fenestra ovalis, and the columella auris passes from the latter to the tympanic membrane (for details see account of orders). A cutaneous fold above the tympanic membrane of crocodiles represents the first trace of an external ear.

The **olfactory organ** presents, particularly in the *Chelonia* and *Crocodylia*, a considerable augmentation of the surface of the mucous membrane, the folds of which are supported by the single cartilaginous turbinal. The lacrymal duct usually opens beneath the turbinal, but it may open into the posterior nares (*Ophidia*) or into the pharynx (*Ascalabota*).

**Jacobson's organs** are absent in *Crocodylia* and *Chelonia*. In *Lacertilia* and *Ophidia* they are present between the nasal sacs and the roof of the mouth (between the turbinates and vomer) as a pair of sacs lined by olfactory epithelium and opening into the mouth just in front of the choanae. They develop as outgrowths of the nasal sacs, are innervated by the olfactory

\* G. Retzius. *Das Gehörorgan d. Wirbelthiere*, vols. 1 and 2, Stockholm, 1881 and 1884.



and trigeminal nerves, and are to be regarded as a second olfactory organ especially developed in connection with the mouth. The tongue is always well developed. In snakes and many lizards this organ serves for feeling and in other cases, e.g. the chameleon, for the prehension of food.

**Alimentary canal.** Teeth are usually present on the premaxillae, maxillae, and dentary, and frequently on the palatine and pterygoid. They are continually replaced, and are pleurodont, acrodon, or thecodont (p. 343). They are conical or hooked, and are adapted for prehension not for mastication (except in some extinct forms). In *Chelonia* teeth are absent, being replaced by the horny epidermal beak-like covering of the jaws.

True salivary glands are usually absent. There is a sublingual in *Chelonia*. Labial glands, both upper and lower, and palatal and lingual glands are frequently present. The poison glands of snakes are upper labial.

The alimentary canal presents no remarkable features. The large intestine is short and often has a small caecum. It leads into the cloaca which receives the urinogenital ducts and in *Lacertilia* and *Chelonia* an allantoic bladder. The anus is a transverse slit in lizards and snakes, a longitudinal slit or a roundish opening in chelonians and crocodiles.

The Reptilia breathe exclusively by lungs, which have the form of spacious sacs with alveoli in the walls (snakes, lizards), or the cavity is much broken up and the lungs are spongy (*Chelonia*, *Crocodylia*). The trachea is long and differentiated in front into a larynx which opens into the pharynx by a slit-like glottis. An epiglottis is found in many tortoises, snakes and lizards. Vocal chords are present only in chameleons, geckos and crocodiles.

In lizards and crocodiles peculiar adhesions may be formed between the lungs and the liver. In crocodiles \* these are extensive and complicated and constitute a diaphragmatic membrane separating the pleural cavities from the general body-cavity.

**Vascular system.**† In all reptiles the heart consists of a

\* Butler, *P.Z.S.* 1889, p. 452.

† Sabatier, *Le Coeur*, Montpellier, 1873. Röse, *Morph. Jahrb.*, 16, 1890, p. 27. G. Fritsch. *Arch. f. Anat. and Physiologie*, 1869, p. 654.

sinus venosus, two auricles and, except in crocodiles, of a single ventricle. It therefore resembles the amphibian heart, but it differs from this in the absence of a conus arteriosus and in the fact that the division of the ventral aorta which has commenced in the Amphibia (particularly in the Anura) is completed and the ventricle gives off three separate arteries, the right and left systemic aortae and the pulmonary.

Both right and left systemic aortic arches persist, but the right is the most important and alone gives off the carotids and subclavians. The left arch either gives off no vessels, or at most only the coeliac artery (*Chelonia*, *Crocodylia*, Fig. 179) close to its union with the right arch. In the *Crocodylia* the ventricular septum is complete and there are two separate ventricles. Of these the right gives off the pulmonary artery and the left systemic aorta, while the right aorta arises from the left ventricle. But the separation of the two sides is not complete, for the two systemic aortae communicate by a small aperture, the *foramen Panizzae*, where they cross one another, just beyond the semilunar valves. The venous system\* is very similar to that of Amphibia. There are two superior venae cavae (ductus Cuvieri), an inferior vena cava which arises in the kidney, and a renal-portal system, which however is reduced in *Chelonia*, the greater part of the blood of the iliac veins passing to the liver. There is a single or double anterior abdominal vein which joins the portal system. All the venous blood of the hind end of the body passes through the kidneys or the liver.

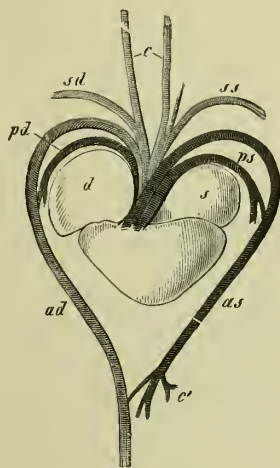


FIG. 179.—Heart and Arteries of a Chelonian (*Chelydra*). *d* right, *s* left auricle; *c* carotid; *ad*, right, *as* left aortic arch; *pd* right, *ps* left pulmonary artery; *cl* coeliac artery; *sd* right, *s* left subclavian artery (from Gegenbaur).

In the snakes and lizards the anterior abdominal vein is single, and does not anastomose with the caudal and iliac veins, which are distributed

\* Rathke, *Bau u. Entwick. des Venensystem der Wirbelthiere*. Königsberg, 1838. Hochstetter, *Morph. Jahrb.*, 13, 17, and 19.

entirely to the kidney. In crocodiles and chelonians the caudal veins bifurcate in front and are continued as the two anterior abdominal veins, which receive the iliac veins. In the crocodile the renal-portal veins start from a transverse vessel which connects the two branches of the caudal.

There is an imperfect septum in the sinus venosus. The interauricular septum is always complete. The ventricular cavity is largely broken up by muscular trabeculae, the central clear space being not very large. The interauricular septum reaches right down to and divides the auriculo-ventricular opening into a right and left division (Fig. 180). To the posterior free edge of this septum are attached two valves ( $v$ ,  $v'$ ), one guarding the right auriculo-ventricular aperture and the other the left; these are the only auriculo-ventricular valves, except in crocodiles (see below). The dorsal and ventral ends of these valves are attached to the dorsal and ventral wall of the ventricle by muscular bands, which constitute together with the valves an incipient septum dividing the ventricle

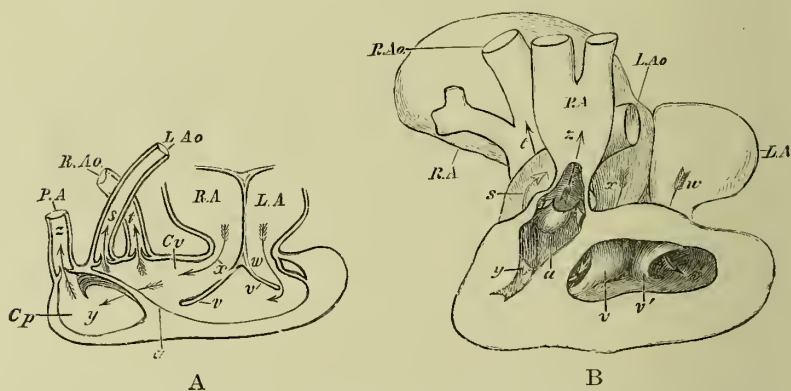


FIG. 180.—The heart of a turtle (*Chelone midas*). A, a diagram explanatory of the arrangement of the cavities and vessels. B, a drawing from nature, the ventral face of the ventricle being laid open (after Huxley).  $a$  muscular flap projecting from the ventral wall and forming an incomplete septum dividing the cavum venosum  $C.v$ ;  $C.p$  part of the cavum venosum from which the pulmonary artery rises;  $L.A$  left,  $R.A$  right auricle;  $L.Ao$  left,  $R.Ao$  right aorta;  $P.A$  pulmonary artery;  $s$  arrow showing course of blood in left aorta,  $t$  in right,  $z$  in pulmonary artery and  $y$  behind the incomplete septum;  $v$ ,  $v'$  the right and left auriculo-ventricular valves;  $w$ ,  $x$  arrows in auriculo-ventricular openings.

into a right and left portion. Of these the right, which is the larger and receives the opening of the right auricle, is called the cavum venosum ( $C.v$ ), while the smaller left receives the left auricle and is called the cavum arteriosum. The cavum arteriosum gives off no vessels; whereas the cavum venosum gives off three—a dorsally arising pulmonary artery, and a right and left systemic aorta. The left systemic aorta arises to the right of the other and crosses to the left side (Fig. 180), passing ventrally to it. The cavum venosum is imperfectly divided into two by a muscular projection of its ventral wall ( $a$ ). From the right side of this projection, from the cavum pulmonale as it may be called, arises the pulmonary artery, from the left the two systemic arches. When the ventricle contracts the free edge of the imperfect septum so constituted meets the dorsal wall of the ventricle and the heart becomes functionally divided for the

moment into two chambers. Of these the right being nearer to the opening of the venous auricle is charged with venous blood which it delivers into the pulmonary artery, whereas the left contains mixed blood near the septum and arterial blood in the *cavum arteriosum*. The former will pass mainly into the left aortic arch, the latter into the right, from which the carotids and subclavians spring. A proper distribution of blood is thus assured, the carotids receiving arterial blood only. In the crocodile the ventricle is double and its cavity much clearer of muscular trabeculae than in the other orders. Further the auriculo-ventricular openings are guarded not only by the mesially attached pocket-valve, alone found in other reptiles, but also by a muscular flap of the ventricular wall (like that in the right ventricle of birds).

The vascular arches which persist in reptiles are the 3rd, 4th, and 5th postoral.\* The vessel of the third arch (first branchial of fishes) becomes the carotid: in *Lacertilia* it usually retains its connection dorsally with the next arch (Fig. 181) by a vessel which is called a *ductus Botalli*. In *Chelonia* (Fig. 179) the fifth or pulmonary arch retains its connection with the preceding (fourth or systemic), so that the *ductus Botalli* is between the fourth and fifth arches.

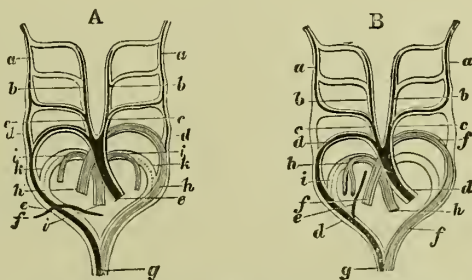


FIG. 181.—Diagrams illustrating the metamorphosis of the vascular arches in a lizard *A*, and snake *B* (from Balfour). *a* internal, *b* external, *c* common carotid; *d* in *A*, ductus Botalli between third and fourth arches, in *B*, right aortic trunk; *e* in *A*, right aortic trunk, in *B* vertebral artery; *f* subclavian in *A*, left aorta in *B*; *g* dorsal aorta; *h* in *A* left aorta, in *B* pulmonary artery; *i* pulmonary artery in *A*, ductus Botalli in *B*; *k* connection, lost in the adult between pulmonary and systemic arch.

The **lymphatic system** is similar to that of *Amphibia*. There are some wide lymphatic spaces, and posterior lymph hearts opening into the ischiadic veins are present. Lymphatic glands are absent, except in crocodiles in which there is one in the mesentery.

Spleen, paired thymus, thyroid, and suprarenal bodies are always present.

The **kidneys** are usually lobed structures placed posteriorly.

\* It is maintained by some anatomists that the persisting arches are the third, fourth, and sixth, the fifth early undergoing atrophy. In this case the pulmonary artery of reptiles will be derived from the vessel of the sixth postoral arch as in *Amphibia* (see Boas, *Morph. Jahrbuch*, 13, 1887, p. 115).

They correspond to the posterior thick part of the amphibian kidney. The ureter, which is to be regarded as the united collecting tubes of the metanephros of Amphibia, opens into the cloaca, and the urine is often a whitish mass of firm consistency containing a considerable quantity of uric acid. There is a bladder in *Lacertilia* and *Chelonia*.

In the **reproductive organs** the mesonephros of Amphibia and its duct have become entirely taken over into the service of the testis. The mesonephros (wolffian body) has lost its kidney structure and become incorporated into the testis as a portion of the epididymis, while the mesonephric duct (pronephric, primitive longitudinal duct) forms the rest of the epididymis and vas deferens. In the female the mesonephros and its duct atrophy or persist as a small vestige (Rosenmüller's organ, canal of Gaertner), and the duct of Müller persists as the oviduct. The oviducts begin with a wide abdominal ostium, have a sinuous course and glandular walls, and open into the cloaca.

The eggs are large and much distended with yolk as in birds. They are fertilized in the oviduct and receive a coating of albumen and a shell (membranous or calcareous) in their passage down the latter. They are usually laid as soon as the shell is formed and undergo the greater part of their development outside the mother, who as a rule takes no further trouble about their fate, but in a few forms they are retained for a considerable time in the oviduct, sometimes till the embryonic development is completed.

The males always possess organs of copulation, to which similarly arranged but smaller structures (*clitoris*) correspond in the female. In snakes and lizards these organs are paired and consist of protrusible hollow pockets of the cloaca. When protruded their surface is traversed by a groove which conveys the sperm from the genital openings in the cloaca. In *Chelonia* and *Crocodylia*, a median erectile penis, consisting of two corpora cavernosa and a terminal glans and supported by fibrous bands, is attached to the ventral wall of the cloaca.

The developmental history\* of reptiles is very similar to that of

\* C. E. v. Baer, *Entwicklungsgeschichte der Thiere*, II. Königsberg, 1837. H. Rathke, *Entwicklungsgeschichte der Natter*, Königsberg, 1839. *Id.*, *Die Entwickl. der Schildkröten*, Braunschweig, 1848. *Id.*, *Unters. üb. d. Entwickl. u. d. Körperbau der Crocodile*, Braunschweig, 1866. L. Agassiz, *Embryology of the Turtle*, *Contributions to the Natural History of the United States*, II, Boston, 1857.



birds. The cleavage is meroblastic, and the embryo is provided with an amnion and allantois. The amnion is a purely embryonic structure, but the allantois is the cloacal bladder which is precociously developed and enormously enlarged as the embryonic respiratory organ.

Reptiles are cold-blooded. In the cold and temperate regions they fall into a kind of winter sleep, and in hot climates there is a summer sleep which comes to an end with the beginning of the rainy season. Most of them are very tenacious of life and can exist a long time without food and with limited respiration. The power of reproducing lost parts exists (e.g. the tail in lizards), but is less than in Amphibia.

They first make their appearance in the Lower Permian (*Protorosaurus*). In the Secondary Period they obtained an enormous development both in variety of form and in size. In the Tertiary Period they declined. There are about 3,500 living species at present known. They are divided into nine sub-classes, the interconnections of which are somewhat complicated. They may be arranged as follows:—

Sub-class 1. *Rhynchocephalia*. Permian to present day.

„ 2. *Lepidosauria*.

Order 1. *Dolichosauria*, Cretaceous.

„ 2. *Mosasauria*, Cretaceous.

„ 3. *Lacertilia*, Jurassic to present day.

„ 4. *Ophidia*. Cretaceous or Eocene to present day.

Sub-class 3. *Crocodylia*. Triassic to present day.

„ 4. *Dinosauria*. Triassic to Cretaceous.

„ 5. *Pterosauria*. L. Jurassic to Cretaceous.

„ 6. *Ichthyosauria*. Triassic to Cretaceous.

„ 7. *Plesiosauria*. Triassic to Cretaceous.

„ 8. *Anomodontia*. Permian and Triassic.

„ 9. *Chelonina*. Triassic to present day.

Sub-class 1. RHYNCHOCEPHALIA.\*

*Lizard-like creatures with biconcave vertebrae, immoveable quad-*

\* A. Günther, "Anatomy of Hatteria," *Phil. Trans.* 167, 1867, p. 595. G. Osawa, a series of papers on the anatomy of Hatteria in *Arch. f. mic. Anat.*, vols. 47, 1896, p. 570; 49, 1897, p. 113; 51, 1898, p. 481; 52, 1898, p. 268. F. Siebenrock, Zur Osteologie des Hatteria-Kopfes, *Sitzb. Akad.*

rate, upper and lower temporal arcades, acrodont teeth, 5-toed limbs, and a parietal organ. The premaxillae are paired, the mandibular symphysis usually ligamentous, the skin has horny scales, and the vertebrae frequently contain persistent remains of the notochord. Anal opening transverse.

The living genus *Sphenodon* may be taken as the type of the group. The body is lizard-like in appearance, possessing a scaly skin, a long tail and four pentadactyle limbs adapted for walking. The vertebrae are amphicoelous, the cavities between the centra containing persistent vestiges of the notochord, as in the geckos. Intercentra in the form of subvertebral wedge-bones or chevrons are present on all the vertebrae. The atlas and axis are as in other living reptiles and there is a so-called proatlas as in crocodiles (p. 373). The caudal vertebrae are divided by a septum as in lizards, and the tail when lost is reproduced. The ribs are single-headed, and some of them possess cartilaginous uncinat processes. There is a median sternum to the anterior end of which are attached the coracoids and the interclavicle. Abdominal ribs are present in the form of numerous transverse rows of small splint-bones (three in each row), between the sternum and the pelvis. In the skull (Fig. 182) there are paired frontals, parietals and premaxillaries, and a pineal (parietal) foramen. The upper temporal arcade is formed by the postorbital and squamosal, the lower by the jugal and quadrato-jugal which reaches back to the quadrate. The posterior border of the orbit is formed by the postfrontal, post-orbital and jugal. There is an epipterygoid extending from the parietal to the pterygoid and quadrate. The palate is almost entirely bony; the internal nares are narrow and elongated, immediately external to the vomers, and there is a vacuity between the median parts of the pterygoids. The pterygoids reach back to and are suturally united with the quadrates which are fixed. The bottom of the orbit is almost completely osseous. The dentary pieces of the mandible are united by ligament and not suturally.

Wien, 102, 1893, p. 250 (and in *Ann. Mag. Nat. Hist.* (6), 13, p. 297). G. B. Howes and H. Swinnerton, "Development of the skeleton of *Sphenodon*," etc., *Trans. Zool. Soc.*, 16, 1901 (contains a bibliography). H. S. Harrison "Development and succession of teeth in *Hatteria*," *Q.J.M.S.*, 44, 1901, p. 161. A. Dendy, *Outlines of the Development of the Tuatara*, *Q.J.M.S.* 42, 1899, p. 1. For extinct forms see Woodward, Zittel, *op. cit.*

The dentition is acrodont, and the teeth are fused with the subjacent bone. The premaxillary teeth, and the downwardly curved premaxillae with which they are fused, have the appearance, especially when worn down, of a pair of rodent-like incisors. There is a row of small triangular teeth on the maxilla and another on the palatine. The single row of mandibular teeth

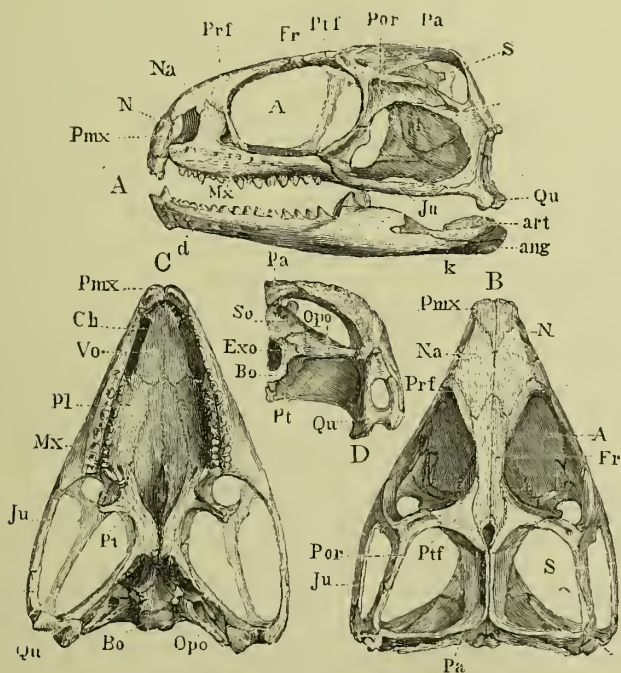


FIG. 182.—*Sphenodon punctatus*, skull A from the side B from above, C from below, D from behind (after Gunther, from Zittel). A orbit; Ang angular; art articular; Bo basioccipital; Ch internal nares; d dentary; Exo exoccipital; Fr frontal; Ju jugal; K surangular; Mx maxilla; N external nares; Na nasal; Opo opisthotic; Pa parietal; Pl palatine; Pmx premaxilla; Por postorbital; Prf prefrontal; Pt pterygoid; Ptf postfrontal; Qu quadrate; Qu Ju quadrato-jugal; S superior temporal fossa; Sq squamosal; So supraoccipital; Vo vomer.

bite between these two rows in the upper jaw. In some young specimens there are a few small teeth on the vomers. The pterygoids are edentulous.

There is a T-shaped-interclavicle and a clavicle, and the coracoid is without fenestrae. The humerus has an entepicondylar as well as an ectepicondylar foramen. The carpus has ten separate bones. The pelvis is somewhat lacertilian though the

ilium is more erect than in that group. There are five digits on each limb.

The tympanic membrane is not visible externally, but on removing the skin in the aural region there is found a strong aponeurotic expansion which represents it. The tympanic cavity is represented by a large pharyngeal recess. The hyoid arch is continuous with the outer cartilaginous end (extrastapedial) of the columella,\* which is in contact with the parotic process of the skull. It would thus appear that the extrastapedial cartilage in *Sphenodon* is the proximal end of the hyoid arch. In their internal anatomy generally they resemble lizards, the most important difference being the absence of copulatory organs. The anus is a transverse cleft as in snakes and lizards. The parietal organ is well developed (Figs. 178, 189, and p. 344).

*Sphenodon* was formerly common on the main islands of New Zealand, but is now restricted to some small islets in the Bay of Plenty. It appears to be on the verge of extinction. The animals inhabit burrows and are nocturnal in habit. They are carnivorous and as a rule slow in their movements. They can however run fast and can defend themselves with some vigour. They lay eggs from November to February. Though the young appear to be almost fully developed in August, they do not hatch out until thirteen months after oviposition.

There can be little doubt that the *Rhynchocephalia* are more closely allied to the *Lacertilia* than to other living reptiles. This is shown by the general form of the body, the presence of a parietal organ, the structure of the respiratory organs, of the vascular system, and by the internal anatomy generally; and on the whole by the skeletal system. There are however important points of difference. The most noteworthy of these are the form of the palate (particularly the apposition of the pterygoids), the immoveability of the quadrate, the presence of a lower temporal arcade in the skull; the erect ilium and the presence of uncinatè processes and abdominal ribs. In these features they may be said to approach the *Crocodylia*, and in some of them the *Dinosauria* and *Chelonina*. The amphicoelous character of the vertebrae is found again in the Geckos, but the absence of copulatory organs is a unique feature among reptiles: on the whole it seems advisable in the present state of knowledge to associate them as was done by Günther and Huxley with the *Lacertilia* and *Ophidia*, but it must not be forgotten that they do present certain skeletal features which are not present in lacertilians, but which are found in other reptilian groups, particularly in crocodiles.

\* Huxley, *P.Z.S.*, 1869, p. 391.

They make their appearance in the Permian and they are therefore the oldest known reptiles. For this reason and also on account of the above-mentioned resemblances to other reptilian groups they have been regarded by some authors as an ancestral group or at least as being closely allied to the ancestors of reptiles generally and possibly of birds. We do not share this view. The *Rhynchocephalia* are essentially reptilian, i.e. they present so far as we know them all the typical features of reptilian organisation in full development. This is hardly what we should expect if they were an ancestral group. It is true that the earlier forms from the Permian are very imperfectly known, but this fact can hardly be alleged as an argument in favour of the view that they are ancestral. Doubtless the view would not have been put forward had it not been for the earliness of their appearance as fossils. But arguments based on this fact lose much of their weight when we consider the necessary imperfection of the geological record. The fact that fossil remains of any particular animal are not found in any particular strata cannot be regarded as evidence of the non-existence of the animal. If it could we should have to regard the living genus *Sphenodon* as being totally disconnected with the other genera of its family, for the family *Sphenodontidae* is not found fossil after the Jurassic period. Again the Chelonians make their appearance in the Triassic strata with all the specialities of the order. When we consider the small change which has taken place in the organisation of the Chelonians or indeed of the Crocodilia since the Triassic age, is it reasonable to suppose that they were evolved from sphenodon-like forms in the interval comparatively short which elapsed between the laying down of the Permian and Triassic strata? The Chelonians of the Trias must have had predecessors. It can hardly be regarded as an unreasonable view to hold that their remains perhaps in a less specialised form will some day be found in the Permian or perhaps even earlier; and even if they are never found in those earlier strata, it is hardly open to us to argue that they did not exist before the Triassic age, unless indeed we give up the evolution hypothesis altogether and assume that they came into existence suddenly and without predecessors. And if they existed before the Triassic age the argument that the Rhynchocephalia are ancestral to them, in so far as it is based on their antiquity, is much weakened, if it does not completely fall to the ground.

As already stated the Rhynchocephalia are represented at the present time by the genus *Sphenodon* which lives in New Zealand, and so far as we know has not been found in the fossil state.

The group may be classified as follows :—

**Protorosauridae.** Prenaxillae, maxillae and mandibles with conical teeth either implanted in shallow pits or fused with the jaws. Vomer covered with small teeth. Interclavicle rhombic in front, prolonged behind. Permian and Trias. *Palaeohatteria* Credner, long-tailed small lizards 45 cm. in length, vertebrae amphicoelous with continuous notochord, abdominal ribs as numerous small oat-shaped scutes, Lower Permian, near Dresden. *Protorosaurus* H. v. Meyer, the Thuringian lizard, to 6 or 7 feet; with long neck; skull and limb girdles imperfectly known, intercentra in the neck only, vertebrae amphicoelous, neurocentral suture obliterated, limbs well developed, Upper Permian of Thuringia; *Telerpeton* Mantell, Elgin Sandstone (Trias).

Fragments from the Permian of Texas and the Lower Permian of Bohemia known as *Clepsydrops*, *Dimetrodon*, *Naosaurus*, etc. seem to be allied here. They have been classed as *Pelycosauria* and many of the genera have enormous neural spines with lateral branches.



The remaining families are sometimes classed as *Rhynchocephalia vera*.

**Mesosauridae.** With numerous fine, brush-like teeth in the jaws; neck long, with short hatchet-shaped ribs; tarsus with two bones in the proximal row. Permian and Trias. *Mesosaurus* Gervais, Lower Trias of S. Africa. *Stercosternum* Cope, Permian of Brazil.

**Champsosauridae.** Large aquatic reptiles with gavial-like head from the Cretaceous and Lower Eocene of N. Amer. and the Lower Eocene of Europe. *Champsosaurus* Cope.

**Rhynchosauridae.** Skull massive with edentulous bent down beak-like premaxillae; upper jaw and palate with 3 or more rows of pyramidal teeth; Trias. *Rhynchosaurus* Owen, Upper Trias, Warwickshire; *Hyperodapedon* Huxley, 6 feet in length, no parietal foramen, Elgin Sandstones and Indian Trias.

**Sauranodontidae.** Upper Jura of France.

**Sphenodontidae.** Upper Jura and present time. It is interesting to note the long period (Cretaceous and Tertiary) in which these reptiles have not been found. *Homalosaurus* v. Meyer, very like *Sphenodon*, but ribs without uncinate, without intercentra in the dorsal region, without entepicondylar foramen in the humerus, Upper Jurassic; *Ardeosaurus*, *Acrosaurus* v. Meyer; *Euposaurus* Jourdan; *Pleurosaurus* v. Meyer; *Sphenodon* Gray (*Hatteria* Gray), living, N. Zealand.

## Sub-class 2. LEPIDOSAURIA (SQUAMATA).

*With procoelous, rarely amphicoelous vertebrae, and with horny scales; sacrum of two vertebrae or absent; ribs single-headed; abdominal ribs absent. Quadrate moveable, attached to the skull by its proximal end only; lower temporal arcade absent, palate with many vacuities; pterygoids not reaching to the vomers.*

The Lepidosauria comprise the orders *Lacertilia* and *Ophidia* and the extinct groups of aquatic forms, the *Dolichosauria* and the *Mosasauria*.

### Order 1. DOLICHOSAURIA.

*Small aquatic snake-like forms with well developed limbs and limb-girdles; vertebrae with zygantra and zygosphenes; teeth pleurodont; lower jaw with sutural symphysis.*

This order includes the long-necked Cretaceous form *Dolichosaurus* Owen with 17 cervical vertebrae; and the genera *Aigialosaurus*, *Pontosaurus*, etc. probably belong to it.

### Order 2. MOSASAURIA.\*

*Large extinct marine reptiles, with two pairs of clawless five-toed limbs. Skull varanus-like with a pineal foramen; lower jaw with ligamentous symphysis. Sacrum absent, the ilia not reaching the vertebral column.*

The vertebral column always contains more than 100 vertebrae, distinguishable into cervical, thoracic, lumbar and caudal. Zygosphenes and zygantra are occasionally, but rarely, present. The skull has a superior

\* Sometimes called *Pythonomorpha*.

temporal arcade and resembles that of *Varanus*. It has an epipterygoid, but resembles snakes and Rhynchocephalia in having a ligamentous symphysis to the lower jaw. Further there is a joint in each ramus just behind its middle joint. Teeth are present on both jaws and on the pterygoids. The limbs are paddle-shaped; they and their girdles are fairly normal, but the long bones are much shortened and the digits often have an increased number of phalanges and are without claws. There is no clavicle, and the ilia are loosely, if at all, attached to the vertebral column. They usually reach a considerable size (to 25 feet or more) and in their general appearance recall that of the toothed whales. They are found in the Upper Cretaceous of Europe, N. and S. America, and N. Zealand.

*Mosasaurus* Conyb. (*Leiodon* Owen), Upper Cretaceous of Maestricht (Holland), of Belgium, France, N. Germany and N. America. *Platecarpus* Cope, N. Amer.; *Clidastes* Cope (*Edestosaurus* Marsh), N. Amer.; *Tylosaurus* Marsh (*Leiodon* Cope), N. Amer.; *Hainosaurus* Dollo, Belgium; *Taniwhasaurus* Hector, N. Zealand.

### Order 3. LACERTILIA \* (AUTOSAURI).

*Reptiles with horny epidermal scales, moveable quadrate bones, transverse anal opening, paired copulatory organs, a cloacal bladder, and two sacral vertebrae. The skull is without a bony quadrato-jugal arcade.*

The lizards always have an elongated and sometimes a snake-like body. As a rule there are four limbs, which however scarcely carry the body raised from the ground. In locomotion they are used principally for pushing the body forward, but they may also be used for clinging (*Chamaeleon*), climbing (geckos), and digging. They usually end with five clawed digits. They are sometimes so short and reduced, that they have the appearance of stumps applied to a serpent-like body, and are without separate digits (*Chamaesaura*). In other cases vestiges of the posterior limbs alone exist (*Pseudopus*, *Pygopus*, Fig. 183), or anterior limbs alone are present (*Chirotes*), or finally external limbs may be entirely absent (*Anguis*, *Anelytropidae*, *Amphisbaena*). The pectoral and pelvic girdles are however present, and in all lizards except *Amphisbaena* there is at least a trace of the sternum,

\* Tiedemann, "Anatomie und Naturgeschichte der Drachen," Nurnberg, 1811. Wiegmann, "Herpetologica mexicana, Pars I, Saurorum species amplexens," Berlin, 1834. Fischer, "Die Gehirnnerven der Sauriern" *Abh. a. d. Geb. der Naturw. Hamburg*, vol. 2, 1852. Rathke "Untersuchungen ueber die Aortenwurzeln u. die von ihnen ausgehenden Arterien der Saurier," *Denkschr. der Wiener Akad.*, 15, 1857. E. Schreiber, "Herpetologica europaea," Braunschweig, 1875. G. A. Boulenger, "Catalogue of the Lizards in the British Museum," London 1885, 3 vols. E. D. Cope, "The Crocodilians, Lizards and Snakes of N. America," *Report of the U. S. National Museum*, 1898, pp. 153-1,270, 1900. Huxley, Zittel, Gadow, *op. cit.*

which increases in size as the anterior limbs become more developed, and then serves for the attachment of a correspondingly greater number of ribs. Except in the *Amphisbaenidae* and a few other lizards the tail is long. The limbless forms and those with reduced limbs are by no means specially related to one another. They turn up in many of the families and the loss or reduction of the limbs seems to be associated with some special habit of life, such as burrowing or living among stones and thick vegetation.

Most lizards have an upper and lower eyelid and a nictitating membrane, but in the *Amphisbaenidae* and *Geckonidae* and some *Scincidae* the eyelids are fused over the eye as in snakes and there is a cavity lined by conjunctiva between them

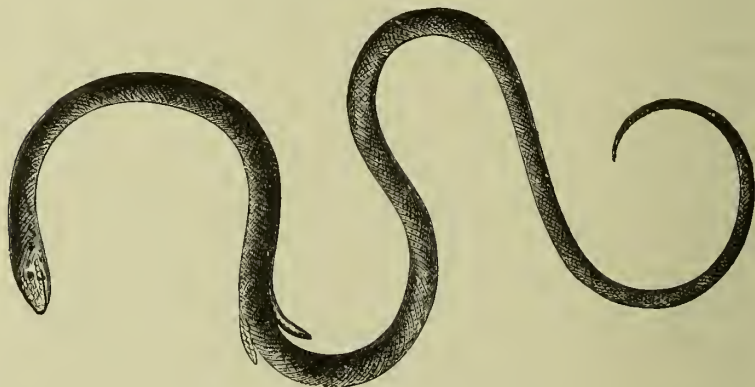


FIG. 183.—*Pygopus lepidopus* (Règne animal).

and the cornea. In some *Scincidae* the centre of the lower eyelid is transparent and can be raised over the eye without hindering the sight. In chameleons the single eyelid is circular, consisting of a muscular ring of skin with circular opening. An exposed tympanic membrane is usually present, but in *Amphisbaenidae* both it and the tympanic cavity are absent, and in many lizards (*Anguis*, *Anelytropidae*, *Chamaeleontidae* etc.) the tympanic membrane is covered by the skin or absent.

The integument of lizards resembles in its general features that of snakes, but presents much greater variety. As a general rule it is scaly. The scales consist of horny epidermal plates placed on dermal papillae and frequently overlap.

The latter may in some forms (*Scincidae*, *Anguidae*, on the head only in *Lacertidae*) develop bony plates (osteoderms), which on the head may coalesce with the subjacent bones. The scales on the head are arranged much as in snakes and the same nomenclature is used in describing them. The scales may have the form of chagrin-like granules or of variously formed tubercles. In the *Amphisbaenidae* the skin is soft and scaleless. The horny layer of the epidermis periodically peels off in flakes, or as in *Anguis* etc. in one piece. Cutaneous lobes on the throat and sides of the trunk, and crests on the back and top of the head are often present. Cutaneous glands are present on the inner sides of the thighs (femoral glands, *Fig. 191a, SP*) and in front of the anus, otherwise they appear to be absent. They are tubular structures filled either with a slimy mass or with a short wart-like body of a horny consistency which in the breeding season may project on the surface. They are present in both sexes or only in the males, and are absent in some genera.

Most lizards are capable of changing colour. This is especially seen in the chameleons.

The vertebrae are procoelous except in the *Geckonidae* in which they are amphicoelous. In this family the notochord persists, except in the middle of the vertebrae, throughout the vertebral column. All the vertebrae in front of that carrying the first sternal rib are cervical. There are one or two lumbar, two sacral, and a large number of caudal. The atlas consists of three pieces, one ventral and two dorso-lateral. The odontoid is closely attached to the axis. The two sacral vertebrae are not ankylosed, but they are united by strong ligaments. The anterior caudal vertebrae have *chevron* bones attached to the centra and not to the intervals between; and *subvertebral wedge-bones*, consisting of small separate ossifications found on the ventral surface at the junction of two vertebrae, are often present on other parts of the vertebral column.

In the *Iguanidae* the vertebrae are articulated by zygantra and zygosphenes as in snakes, in addition to the ordinary articulating processes. In many lizards the caudal vertebrae are composed of two halves, an anterior shorter to which the transverse process is attached, and a longer posterior portion. This phenomenon is due to the presence of a thin unossified transverse septum traversing the vertebrae. As is well known, many lizards when seized by the tail have a habit of breaking off the part seized and so escaping. Such breaks always take place at one of the weak

spots caused by these unossified septa. The lost tail is replaced by regeneration, but the new tail (which may be double) has an imperfect skeleton and its scaling may differ from that of the lost part.\*

The ribs are single headed and are attached to the vertebrae between the centrum and the arch; a ligament, however, often passes from the neck of the rib to the neural arch. In the anterior and posterior vertebrae they are often attached to transverse processes. Ribs are found on all the precaudal vertebrae except the atlas and sometimes the next two, and on one or two of the presacral vertebrae (lumbar). The proximal part alone ossifies, the distal part remaining cartilaginous or becoming calcified.



FIG. 184.—Sternum and sternal ribs of *Chamaeleo* (from Gegenbaur). *St* sternum; *Mst* posterior part of sternum, (metasternum); *Co* coracoid; *c, c'* ribs.

The posterior ribs present a peculiar modification in *Draco*, being extremely long and serving to support lateral expansions of the skin, by which the animal is able to perform its flights. In the geckos and chamaeleons the posterior ribs meet each other in the ventral middle line forming complete hoops.

Except in the *Amphisbaenidae* and some other lizards in which the fore-limbs are absent, a variable number of the anterior thoracic ribs are connected by a cartilaginous sternal portion with the sternum.

In all lizards except some of the *Amphisbaenidae* there is at least a trace of a sternum (though as we have seen it is not always connected with the ribs), which increases in size in forms in which the anterior limbs are more developed. The sternum typically consists of a rhomboidal plate of cartilage, from the posterior part of which a single or double prolongation is continued backwards into the wall of the abdomen. A few (two to four) sternal ribs are attached to the rhomboidal plate and the remainder (one to four) to the posterior continuations (Fig. 185).

In the skull (Fig. 186) there is a cartilaginous interorbital septum (except in the *Amphisbaenidae*). The temporal region (exoc-

\* Boulenger, *P.Z.S.*, 1888, p. 351.



cipital, prootic and opisthotic) is prolonged outwards into parotic processes (as in the *Chelonia*), to the outer end of which the quadrate is articulated (usually moveably). There is a small bone at the outer ends of these processes, called the supra-temporal (14). There are no alisphenoids, orbitosphenoids, or presphenoids; this part of the skull wall being mainly membranous with tracts of cartilage. There is in all, except the *Amphisbaenidae* and *Chamaeleonidae* and the genus *Anniella*, a rod-shaped bone—the *epipterygoid*—extending from the parietal

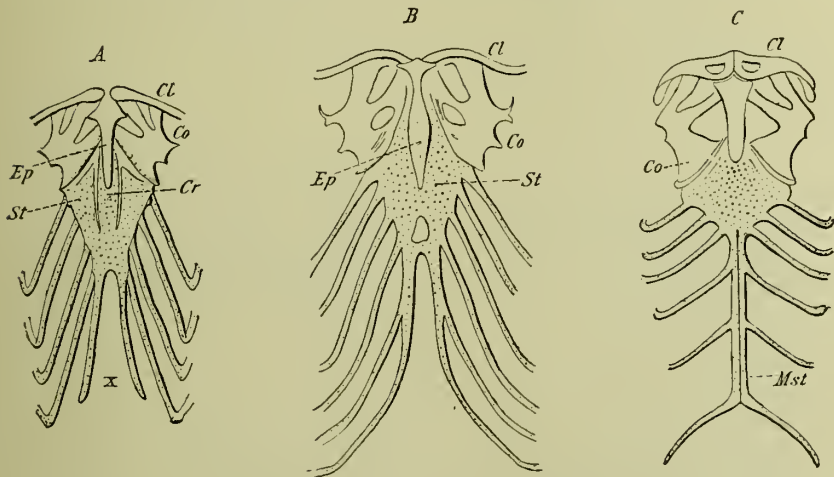


FIG. 185.—Sternum with ribs and shoulder girdle of *A*, *Iguana*; *B*, *Lophiurus*; *C*, *Platydictylus*. *St* sternum; *ep* interclavicle (episternum); *Mst* posterior prolongation of sternum carrying sternal ribs; *Co* coracoid; *Cl* clavicle; *Cr* sternal crest; *X* posterior continuation of sternum without ribs (xiphisternum) (from Gegenbaur).

to the pterygoid on each side, in close contact with the membranous or cartilaginous wall of the skull (23). This bone is sometimes called the columella cranii which is a bad name because it leads to confusion between it and the columella auris. Those lizards which possess it have been called the *Kionocrania*. There is a small ossification in some *Chelonia* between the descending process of the parietal and the pterygoid which seems to correspond to it. The occipital condyle is mainly formed by the basioccipital but the exoccipitals participate. It is double in the *Amphisbaenidae*. The opisthotic is fused with the exoccipital and the epiotic with the supraoccipital, the prootic remaining separate. The parietals are not joined suturally to the

supraoccipital (except in the *Amphisbaenidae* and chameleons), but by fibrous tissue, so that the fronto-parietal part of the skull is usually slightly moveable upon the occipito-sphenoidal part. There is a pineal foramen either in the course of the sagittal suture or between the parietals and frontals. The parietals are usually fused in the adult but remain separate in the geckos. The frontals are usually paired, but may fuse in the adult. A thin splint of bone projects forwards from the basisphenoid beneath the interorbital septum (28); this is a membrane bone fused with the basisphenoid and representing the anterior part of the parasphenoid of Ichthyopsida. The posterior part of the parasphenoid is represented in the embryo by two membrane bones which fuse with the basisphenoid in the adult (*basi-temporals*). The praemaxillae are fused and there is a small bone on each side just above the vomer, in the anterior part of the nasal region called the *septomaxillary* (29). A perforated lacrymal is generally present in the anterior part of the orbit.

The squamosal (9) is attached to the parotic process and extends forward to the postfrontal (except in the geckos) forming the supratemporal arcade and bounding the outer side of the supratemporal fossa (15). The parietal sends out a postero lateral process to the squamosal thus forming the posterior boundary of this fossa. In most lizards the postfrontal (16) is joined to the jugal (6), completing the orbit and closing the supratemporal fossa in front, but in the geckos and *Amphisbaenidae* these bones are separate and the orbit is open behind. The infratemporal arcade is not developed, there being no bony connection between the jugal and quadrate. The bones of the maxillopalatine apparatus are firmly connected with one another and with the anterior part of the skull, but the pterygoids (7) are moveably articulated with the basisphenoid and quadrate. There are two vomers (19) forming the inner wall of the posterior nares. The palatines (4) pass back from these and the maxillaries to the pterygoids, which diverging from one another extend back to the quadrate (except in the chameleons) articulating on the way with lateral (basipterygoid) processes of the basisphenoid. There is a transpalatine (5) passing from the palatine and pterygoid to the maxilla and jugal. In the chameleons the supratemporals (pteric) are much elongated and send backwards and dorsalwards a process which unites with a

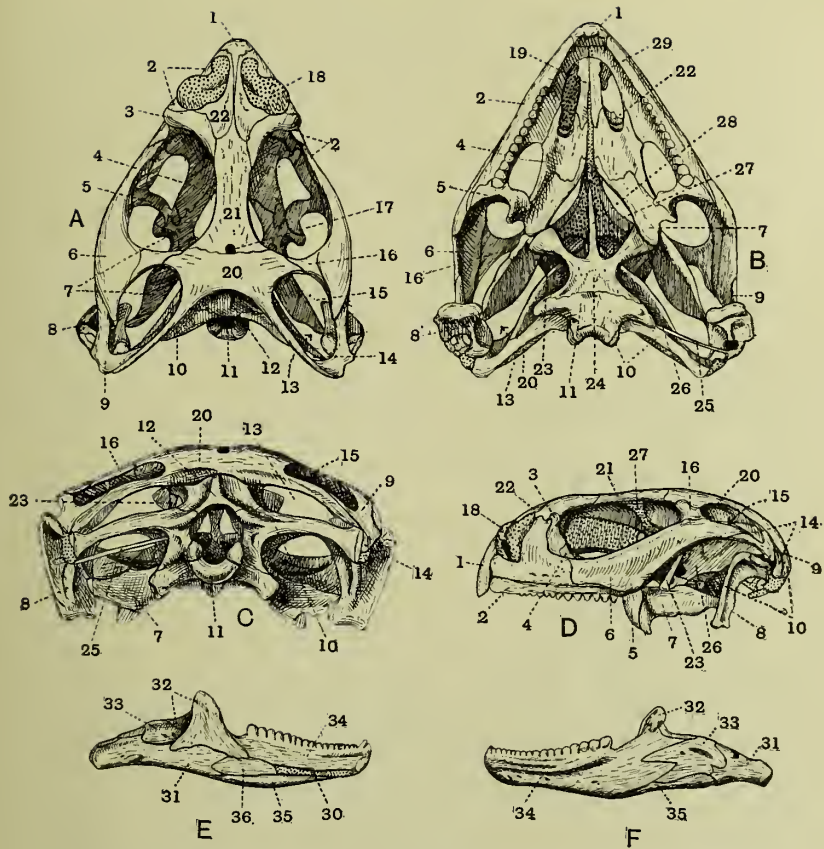


FIG. 186.—Skull of *Uromastix* (after original drawings by J. J. Lister). *A* dorsal, *B* ventral, *C* posterior, *D* side view, *E* and *F* lower jaw. 1 premaxilla; 2 maxilla; 3 prefrontal; 4 palatine; 5 transpalatine; 6 jugal; 7 pterygoid; 8 quadrate; 9 squamosal; 10 exoccipital and opisthotic; 11 basioccipital; 12 supraoccipital; 13 posttemporal fossa; 14 supratemporal bone; 15 supratemporal fossa; 16 postfrontal; 17 pineal foramen; 18 olfactory capsule; 19 vomer; 20 parietal; 21 frontal; 22 nasal; 23 columella cranii (epipterygoid); 24 basisphenoid with which a basitemporal ossification has united; 25 columella auris; 26 prootic; 27 alisphenoid cartilage; 28 parasphenoid; 29 septomaxillary; 30 Meckel's cartilage; 31 articular; 32 coronoid; 33 supraangular; 34 dentary; 35 angular; 36 splenial.

median backward process of the parietals, thus forming the casque of these skulls.

The lower jaw contains the usual six bones (Fig. 186), and the distal end of Meckel's cartilage persists. The two rami are usually firmly connected at the symphysis. The hyoid consists of an elongated body, and two long cornua on each side. It is mainly cartilaginous the posterior cornua being partly ossified. In the geckos the anterior cornua are connected to the skull.

The pectoral girdle is always present, even when the forelimbs are absent, though it may be much reduced and not reach the sternum.\* Typically (Figs. 187 and 188) it consists of a suprascapula, scapula, and coracoid which articulates with the sternum; and of a clavicle, and interclavicle. The scapula and coracoid are partly ossified and fenestrated. Clavicles and interclavicle are absent in the chameleons, and in some of the limbless forms.

The manus usually possesses five digits, in which case the carpus consists of eight bones,—an ulnare, radiale, centrale, and five distal bones.

The pelvic girdle consists of ilia which articulate with the two sacral ribs, and pubes and ischia which meet in a ventral

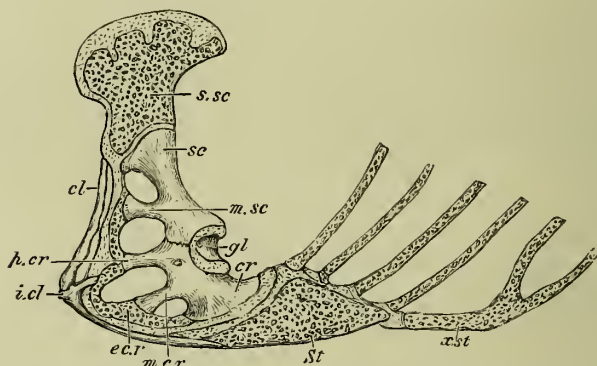


FIG. 187.—Side view of the pectoral girdle and sternum of *Iguana tuberculata* (from Huxley).  
*cl* clavicle; *cr* coracoid; *e.cr* epicoracoid; *gl* genoid cavity; *i.cl* interclavicle; *m.cr* mesocoracoid; *m.sc* mesoscapula; *p.cr* precoracoid; *s.sc* suprascapula; *st* sternum; *x.st* xiphisternum.

symphysis. The pubo-ischiadic foramen is only divided by ligament. There is usually a cartilaginous (or calcified) epipubis, and a cartilaginous continuation of the ischiadic symphysis backward, to support the cloaca (*hypo-ischium* or *os cloacae*). In the limbless forms the pelvic girdle may undergo great reductions, but no part appears to vanish entirely; and the sacral connection is preserved, except in the *Amphisbaenidae*.

The pes usually possesses five digits. In the tarsus there is a tendency to an intertarsal joint. The proximal row consists of two large bones more or less closely united, and articulated

\* M. Fürbringer, "Die Knochen u. Muskeln der Extremitäten bei den Schlangenähnlichen Saurien," Leipzig, 1870.



with the tibia and fibula in a way which allows of very little motion. The distal row contains a cuboid carrying the metatarsals of the fourth and fifth digits, that of the fifth being bent as in *Chelonia*. Other distal tarsals may be present or they may be fused with the metatarsals.

The phalangeal formula of the manus is usually 2. 3. 4. 5. 3, of the pes 2. 3. 4. 5. 4.

**Alimentary canal.** Teeth are present on the premaxillae, maxillae, and dentary, and often on the palate. They may be conical, blade-like, or crushing (*Cyclodus*). They usually become ankylosed to the bone, either by their bases to the edge of the jaw (acrodont), or by their sides just inside the edge (pleurodont). They are never lodged in alveoli (thecodont). The tongue varies considerably. It is generally notched anteriorly and posteriorly drawn out into two processes which may unite behind the glottis, so that the glottis lies in the back of the tongue. In the geckos, *Iguanidae*, *Agamidae*, etc., it is short; in the *Amphisbaenidae*, it is forked. In some forms (*Varanidae*, etc.) it is long, narrow and forked, and provided with a sheath at its base into which it can be retracted. In the chameleons it is very long and clubbed at its end.

Salivary glands are absent, but labial glands opening on the lips are present. There is a gall-bladder, usually a short caecum on the anterior end of the rectum, and the cloaca has a bladder.

The larynx consists of a cricothyroid cartilage and of arytenoid cartilages. The cricothyroid frequently has fontanelles and in *Amphisbaenidae* is represented by two lateral bands of cartilage united by cross bands (as in snakes). An epiglottis is sometimes present. Vocal chords are absent except in geckos and chameleons. The tracheal rings are usually complete. The

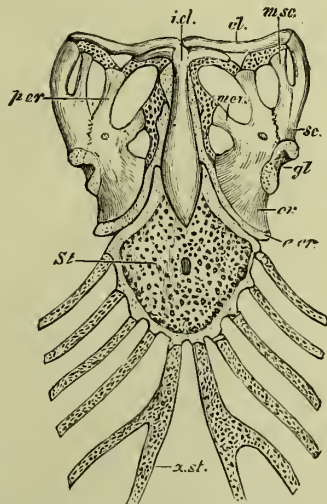


FIG. 188.—Ventral view of the pectoral girdle and sternum of *Iguana*. Letters as in Fig. 187 (from Huxley).



bronchi are short and open into the lungs, which are sacs with honeycombed walls. In the chameleons and some geckos the posterior part of the lungs is produced into narrow diverticula which lie among the viscera and foreshadow the air-sacs of birds. In the snake-like forms the lungs are often of unequal size.

The **brain** has a small cerebellum. Almost all lizards appear

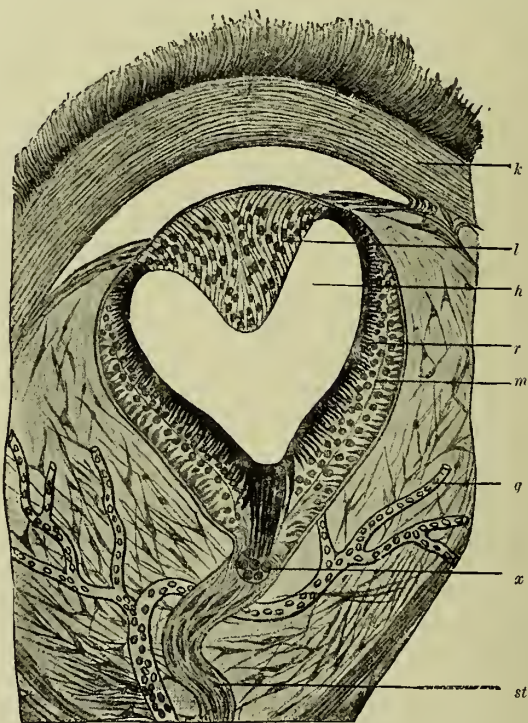


FIG. 189.—Longitudinal section through the connective tissue capsule and the parietal organ of *Hatteria punctata* (after Spencer from Wiedersheim). *g* bloodvessels; *h* cavity of parietal organ; *k* connective tissue capsule; *l* lens-like thickening of the dorsal wall; *r* retina-like part of the parietal organ; *m* molecular layer; *st* cord connecting the organ to the pineal body; *x* cells in *st*.

to possess a parietal organ \* (Fig. 178) lying in the parietal (pineal) foramen or just below it, and often in close relation with the skin. This organ is a vesicle the walls of which may

\* H. W. de Graaf, *Bijdrage tot de ken. van d. Bouw en de Ontwikkeling der Epiphyse bij Amphibien en Reptilien*, Leyden 1886. Spencer, *Q.J.M.S.* 27, 1886. Béranek, *Jen. Zeitschr.*, 1887, 21. Leydig, *Biol. Centralbl.*, 8, 1889, p. 707 and 10, 1890 p. 278; and *Abh. Senckenb. Nat. Ges.*, 16, 1890, p. 441-551.

be a simple epithelium, but more often they present peculiar modifications which recall the structure of an eye. In such cases the dorsal wall is thickened in a manner which suggests a lens-like structure (Fig. 189); while the rest of the wall is pigmented, contains several layers of nuclei and generally presents an aspect which recalls that of a retina. The parietal organ is sometimes quite separate from the brain (*Calotes*, *Seps*, etc., Fig. 190) but more usually perhaps it is connected with the pineal body by a cord of tissue. In *Cyclodus* its cavity is continuous with that of the pineal stalk and so with that of the 3rd ventricle. On account of the eye-like structure and also because it is often attached by a cord of tissue to the pineal body or to the roof of the thalamencephalon just in front of and in close connection with that body, the parietal organ is sometimes spoken of as the "*pineal eye*." The hypothesis as to its nature suggested by this name must be received with caution, as will be explained later on. It is usually placed close to the skin of the top of the head and the skin over it is frequently without pigment. In such cases a portion of the scale immediately overlying it may have a cornea-like appearance. There is however no relation between this external indication and the degree of eye-like development of the parietal organ; e.g. in *Hatteria* in which it has a more eye-like structure than in any other form, there is no external indication of it on the top of the head, while in *Ceratophora*, in which the modified scale is present, there is no parietal organ.

The eye-like character is not always discernible, e.g. in *Cyclodus* in which though it lies in the parietal foramen and has a modified scale over it, it appears to be nothing more than the distended end of the pineal stalk (pineal body). In *Chamaeleon* and others there is no pigment and the walls of the vesicle show no retinal or lens-like differentiations, though the vesicle is connected to the pineal body (or stalk?) by a solid cord. In others again in which the eye-like features can be detected there is considerable variety as to the extent to which they are differentiated, and also as to the presence or absence of a connection (always solid when eye-like structure is present) with the pineal body (Fig. 190). Lastly in forms in which the parietal foramen is closed (e.g. *Gecko*, *Ameiva*, *Ceratophora*) the parietal organ is absent, and the pineal body ends just within the skull-wall.

Developmentally the parietal organ appears to arise as a diverticulum from the anterior side of the pineal body or directly from the cerebral roof immediately in front of this organ (see p. 70).

So far as can be ascertained from experiment the parietal organ has no trace of a visual function, and the interpretation of it as the vestige of a once functional median eye rests entirely upon the evidence of histology. But the histological evidence is by no means conclusive. The nervous

nature of the cord which connects it with the epiphysis has been expressly denied by Leydig, and the fact that pigment may be found in the dorsal (lens-like) part of the wall as well as in the retinal part of the vesicle is not in favour of its optical nature.

Moreover the absence of a nerve connecting it with the brain at least in some if not in all cases, is against the optical interpretation, if we may judge from what we know of the degeneration of the paired eye. Neither can the frequent presence of the so-called cornea above the parietal foramen be regarded as a strong support of the view, for no such corneal area is left in cases of extreme degeneration of the paired eyes. While not attaching any importance to the extreme variability of the organ itself, especially in relation to the "corneal" patch on the skin, the case of *Cyclodus* is difficult to explain on the median-eye hypothesis. For here there is apparently an ordinary pineal body without any eye-like structure and

placed in the parietal foramen, and over it a "corneal" modification of the skin. From these and other considerations it is clear that the interpretation of the parietal organ as an aborted visual organ, though it cannot by any means be dismissed as a baseless hypothesis, must be received with more caution than has hitherto been accorded it.

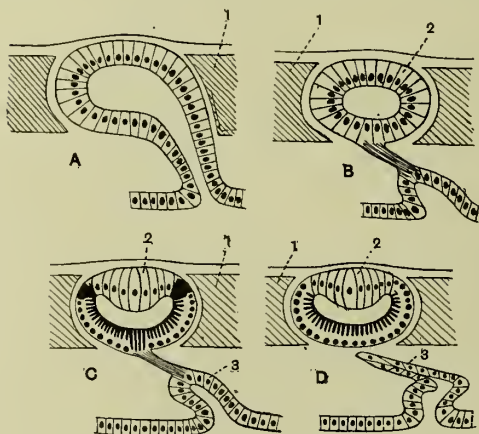


FIG. 190.—Diagrams showing the relation of the parietal organ and pineal body of Lacertilia A, in *Cyclodus*; B, in *Chamaeleon*; C, in most Lacertilia; D, in many Lacertilia (*Calotes*, *Seps*, *Leiopora*, etc.). 2 parietal organ; 3 pineal body; st cord connecting parietal organ and pineal body; 1 parietal bone (after Spencer).

plates in the sclerotic and a vascular projection of the choroid (pecten) into the vitreous humour. Lacrymal and harderian glands are present.

A tympanic cavity is present except in the *Amphisbaenidae* and communicates by wide openings with the pharynx. The columella auris is a bony rod which passes from the fenestra ovalis to the extracolumellar cartilage. The latter is attached to the tympanic membrane. The hyoid arch is far removed from the skull except in the *Geckonidae* in which it is attached to the epiotic, close to an attachment of the extracolumellar cartilage to the same bone. In the chameleons in which there

The eyelids have already (p.336) been described. There is a ring of bony

is no tympanum the extracolumellar cartilage is attached to the inner side of the quadrate.

In the **vascular system** there are a sinus venosus, a single ventricle with an incomplete septum, and three pairs of arterial arches with a ductus Botalli between the carotid and systemic arches (except in the *Varanidae*). The subclavians are given off separately or together by the right arch. The visceral arteries arise from the dorsal aorta. The anterior abdominal vein is unpaired and does not anastomose with the iliac and caudal veins.

Fat bodies between the skin and ventral abdominal muscles are often present. They are largest in the spring at the time of propagation.

The **kidneys** are placed in the posterior part of the body-cavity, and are covered on the ventral side only by peritoneum. They are more or less lobed, are sometimes united with one another and may extend into the caudal region. A cloacal bladder is present.

The testes are oval bodies placed further forwards than the kidneys (Fig. 191). The ureter usually joins the vas deferens of its side and the two open by one opening into the lateral part of the cloaca. The oviducts have the usual arrangement.

There are two penes. They have the form of eversible hollow sacs opening into the posterior wall of the cloaca, and attached by a retractor muscle, passing from their hinder end, to some of the caudal vertebrae. A groove runs to them from the opening of the vas deferens for the conveyance of sperm. Erectile tissue is found in their walls. These organs can be everted through the anus and used as copulatory organs. They are present in both sexes, though less developed in the female than in the male.

Most lizards lay eggs, but a few are viviparous (*Lacerta vivipara*, *Anguis fragilis*, *Seps*, *Chamaeleon*). In some cases the eggs are retained for a part of the development and the young are hatched at a greater or less period after laying. The shell is usually leathery, but may be hard. Most of them are harmless, and are useful by destroying insects. Larger species, as the Iguana, are hunted for the sake of their flesh. By far the greater number and all the larger and more beautifully coloured species inhabit the warmer and hot countries.



Comparatively few fossil forms are known, and these but imperfectly. The oldest, but incompletely known, form is *Macellodon* from the Upper Jurassic (Purbeck Beds). In the Lower Eocene they are more numerous, belonging to the *Varanidae* (*Thinosaurus*), *Anguidae* (*Glyptosaurus*, etc.),

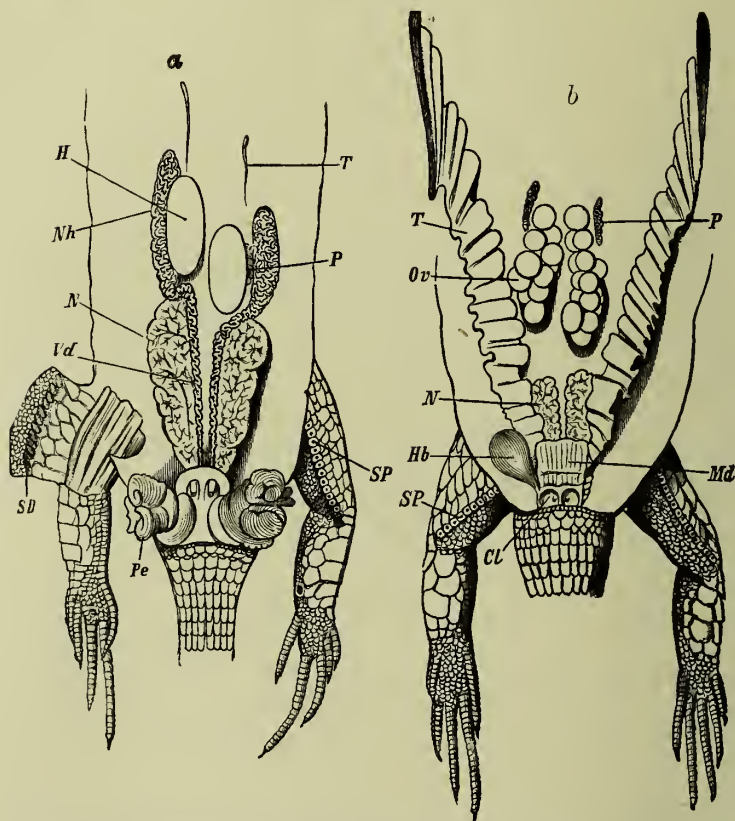


FIG. 191.—Urinogenital organs of *Lacerta agilis* (after C. Heider). *a*, of the male, *b* of the female. *Cl* cloaca; *H* testis; *Hb* urinary bladder; *Md* rectum (cut). *N* kidney; *Nh* epididymis; *Ov* ovary; *P* vestige of wolffian body; *Pe* pencis; *Sd* femoral glands; *SP* pores of femoral glands; *T* oviduct (müllerian) or its vestige in the male; *Vd* vas deferens.

*Iguanidae* (*Iguanavus*) and *Chamaeleontidae*. The lacertilian fossils of the Miocene belong largely to existing genera. There are about 1800 living species.

Sub-order 1. **LACTERTILIA VERA.** The nasal bones enter the border of the nasal apertures, and the pterygoid is in contact



with the quadrate. Clavicles are present when the limbs are developed. The tongue is flattened.

Fam. 1. **Geckonidae** (*Ascalabota*). With amphicoelous vertebrae, with persistent notochord, and a cartilaginous septum, without bony temporal arches; parietals separate; clavicles dilated, loop-shaped proximally; eyelids as small folds not moveable (except *Aelurosaurus* and *Ptenopus*), but the eye is covered with a transparent membrane (possibly the nictitating membrane) behind which the eyeball moves; pleurodont; tongue protrusible; in some genera the vestibule of the membranous labyrinth is much enlarged and, perforating the bone, projects as a bag behind the ear or at the side of the neck; many have adhesive (by production of numerous vacuums) digits, by which they can climb smooth vertical surfaces; they are oviparous (*Naultinus* is said to be viviparous), with hard-shelled eggs; they are quite harmless, mostly nocturnal, found in the hotter parts of all regions; about 50 genera, 270 species, no extinct forms known. *Ptychozoon* Kuhl, of the Malay Islands and Peninsula has cutaneous expansions of the head, body, limbs and tail, which probably act as a parachute; the digits are webbed. Alphabetical list of genera:—

*Aeluronyx*, Seychelles, Madagascar; *Aelurosaurus*, E. Indies, ? Australia; *Agamura*, Persia; *Alsophylax*, Turkestan, Persia; *Aristelliger*, W. Indies, C. Amer.; *Calodactylus*, S. India; *Ceramodactylus*, Persia, Arabia; *Colopus*, S. Afr.; *Chondrodactylus*, S. Afr.; *Dactylchilikion*, S. Afr.; *Diplodactylus*, Australia; *Ebenavia*, Madagascar; *Eurydactylus*, New Caledonia; *Gecko*, Japan, China, E. Indies, New Guinea and neighbouring islands; *Geckolepis*, Madagascar; *Gehyra*, E. Indies, Australia, Mexico, islands of Indian and S. Pacific oceans; *Gonatodes*, trop. Amer., E. Indies; *Gymnodactylus*, borders of Mediterranean, S. Asia, Aust., Pac. Islands, Trop. Amer.; *Hemidactylus*, S. Eur., S. Asia, Afr., trop. Amer., Polynesia; *Heteronota*, Australia; *Homonota*, S. Amer.; *Homopholis*, S. Afr.; *Hoplodactylus*, S. Pacific Islands, S. India; *Lepidodactylus*, E. Indies, Polynesia, S.W. Australia; *Luperosaurus*, Philippines; *Lygodactylus*, Africa, Madagascar; *Microscalabotes*, Madagascar; *Naultinus*, New Zealand; *Nephrurus*, Australia; *Oedura*, Australia; *Pachydactylus*, Africa; *Perochirus*, Philippines, Carolines, New Hebrides; *Phelsuma*, Madagascar, Mauritius etc.; *Phyllodactylus*, trop. Amer., Australia, Afr., islands of Mediterranean; *Phyllopezus*, Brazil; *Pristurus*, N.E. Afr., S.W. Asia; *Ptenopus*, S. Afr.; *Ptychozoon*, E. Indies; *Ptyodactylus*, N. Afr., S.W. Asia, Sind; *Rhacodactylus*, New Caledonia; *Rhoptropus*, S.W. Afr.; *Rhynchoedura*, Australia; *Spathoscalabotes*, E. Indian Archipelago; *Sphaerodactylus*, W. Indies, C. Amer., Colombia; *Stenodactylus*, N. Afr., S.W. Asia, Sind; *Tarentola* (*Platydictylus*) (Fig. 192), W. Afr., borders of Mediterranean, W. Indies; *Teratolepis*, India; *Teratoscincus*, Persia, Turkestan; *Thecadactylus*, trop. Amer., islands of Torres Straits.

Fam. 2. **Eublepharidae**. Similar to foregoing except that the vertebrae are procoelous, the parietals fused, and there are functional eyelids. *Psilodactylus* Gray, W. Afr.; *Eublepharis* Gr., S. Asia, Cent. Amer., S. North-Amer.; *Coleonyx* Gr., C. Amer.

Fam. 3. **Uroplatidae**. Resembling the Geckonidae except that the nasal bones are fused, the interclavicle is small, and the clavicles are not dilated. *Uroplates* Gr., Madagascar.

Fam. 4. **Pygopodidae**. Snake-like, with scales; fore-limbs absent,

hind-limbs as scaly flaps (Fig. 183) with 5 concealed ossified toes ; sternum feeble ; pleurodont ; eyes without lids, unprotected ; tail long ; Australia Tasmania and New Guinea. *Pygopus* Merr. (Fig. 183) ; *Cryptodelma* Fisch. ; *Delma* Gr. ; *Pletholax* Cope ; *Aprasia* Gr. ; *Lialis* Gr.

Fam. 5. **Agamidae**. Acrodont, teeth usually divided into incisors, canines, molars ; tongue short and thick ; orbit closed and temporal fossa bridged ; in *Lyriocephalus* a process of the pre-and-post-frontals unite to form an arch ; osteoderms are absent ; premaxilla single, nasals double, frontal and parietal single ; eyes with lids ; Old World ; about 30 genera, 200 species.

¶ *Acanthosaura* Gr., S.E. Asia ; *Agama* Daud., Afr., S. Asia, S.E. Eur. ; *Amphibolurus* Wagl., Australia ; *Aphaniotis*, Ptrs., Malayasia ; *Aporoscelis*, Blgr., E. Afr. ; *Calotes* Cuv., crest on neck and back, remarkable for changes of colour, India and the Malay Islands ; *Ceratophora* Gr., Ceylon ; *Charasia* Gr., India ; *Chelosania* Gr., Australia ; *Chlamydosaurus* Gr., large frill-like dermal expansion on either side of the neck, runs upon its hind limbs in a semierect position, Australia ; *Cophotis* Ptrs., Ceylon, Sumatra ; *Diporophora* Gr., Australia ; *Draco* L., flying dragon, ribs much prolonged supporting a wing-like dermal expansion, E. Indies ;

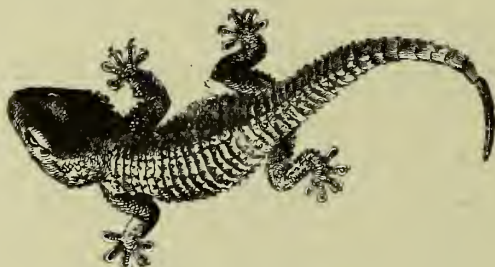


FIG. 192.—*Tarentola mauritanica* (Règne Animal).

*Gonyocephalus* Kaup, E. Indies, Papuasias, Polynesia, N.E. Australia ; *Harpesaurus* Blgr., Java ; *Japalura* Gr., E. Indies, S. China ; *Lirolepis* Cuv., S.E. Asia ; *Lophocalotes* Gthr., E. Indian Arch. ; *Lophura* Gr., E. Indies ; *Lyriocephalus* Merr., chameleon-like, Ceylon ; *Moloch* Gr., mouth

small, teeth in upper jaw horizontal, directed inwards, body covered with large spines, W. and S. Australia ; *Otocryptis* Wieg., Ceylon, S. India ; *Phoxophrys* Hubr., Sumatra ; *Phrynocephalus* Kaup, S.E. Eur., C. Asia ; *Physignathus* Cuv., Australia, Papuasias, Siam ; *Ptyctolaemus* Ptrs., N. India ; *Salea* Gr., S. India ; *Sitana* Cuv., 4 toes, India, Ceylon ; *Tympanocryptis* Ptrs., Australia ; *Uromastix* Merr., spiny-tailed lizards, arid tracts of N. Afr. and S. Asia.

Fam. 6. **Iguanidae**. Closely resemble the Agamidae, but with pleurodont, rarely heterodont (and then but slightly) dentition ; *Chamaeleolis* has teeth on the palatines ; osteoderms are absent on the body, but may be present on the head as in the horn-like tubercles of *Phrynosoma* ; about 50 genera and 300 species ; arboreal, terrestrial, burrowing, semi-aquatic ; some genera have abdominal ribs ; almost entirely American, except *Hoplorus* and *Chalarodon* in Madagascar, and *Brachylophus* in Fiji ; species of *Sceloporus* and *Phrynosoma* are viviparous. *Anisolepis* Blgr., S. Brazil ; *Anolis* Daud., abdominal ribs, digits dilated, with transverse lamellae inferiorly, expert climbers, more than 100 species, trop. and sub-trop. Amer. ; *Amblyrhynchus* Bell, herbivorous, semimarine, living on algae, Galapagos ; *Basiliscus* Laur., high and erectile

crests on the male, C. Amer., *B. americanus* to 3 ft.; *Brachylophus* Wagl., Fiji and Friendly Islands; *Cachryx* Cope, Yucatan; *Callisaurus* Blainv., S.W. N.-Amer.; *Chalarodon* Ptrs., Madagascar; *Chamaeleolis* Coct., Cuba; *Conolophus* Fitz., herbivorous, edible, Galapagos; *Corythophanes* Boie, C. Amer.; *Crotaphytus* Holbr., S. N.-Amer.; *Ctenoblepharis* Tsch., Peru; *Ctenosaura* Wieg., C. Amer.; *Cyclura* Harl., W. Indies; *Diplolaemus* Bell, Patagonia; *Dipsosaurus* Hall, S.W. N.-Amer.; *Enyalioides* Blgr., Veragua to Peru; *Enyalius* Wagl., S. Amer.; *Helocephalus* Phil., Atacama and N.W. la Plata; *Holbrookia* Gir., S. N.-Amer.; *Hoplocercus* Fitz., S. Amer.; *Hoplurus* Cuv., Madagascar; *Iguana* Laur., attain to 5-6 ft., herbivorous, esteemed as food, they live in trees, trop. Amer. and W. Indies; *Laemactus* Wieg., C. Amer.; *Liocephalus* Gr., digits with keeled lamellae, W. Indies and S. Amer.; *Liolaemus* Wieg., Amer. S. of equator, about 25 species; *Liosaurus* D. and B., S. Amer.; *Metopoceros* Wagl., W. Indies; *Norops* Wagl., trop. Amer.; *Ophryoesa* Fitz., S. Amer.; *Petrosaurus* Blgr., Lower California; *Phrynosoma* Wieg., horned toads, N. Amer., and Mexico; *Phymaturus* Gravh., Chili; *Pneustes* Merr., Paraguay; *Polychrus* Cuv., abdominal ribs, colour very changeable, digits with carinated lamellae; trop. Amer.; *Pristidactylus* Fitz., Patagonia; *Saccodeira* Gr., S. Amer.; *Sauromalus* A. Dum., S.W. N.-Amer.; *Scartiscus* Cope, Paraguay; *Sceloporus* Wieg., N. and C. Amer.; *Stenocercus* D. and B., W.S. Amer.; *Strobilurus* Wieg., Brazil; *Tropidodactylus* Blgr., Venezuela and W. Indies; *Tropidurus* Wied., S. Amer., digits with keeled lamellae; *Uma* Baird, Arizona; *Uraniscodon* Kaup, S. Amer.; *Urocentron* Kaup, S. Amer.; *Urostrophus* D. and B., S. Amer.; *Uta* B. and G., N.-Amer. and Mexico; *Xiphocercus* Fitz., trop. Amer.

Fam. 7. **Xenosauridae.** Pleurodont, teeth numerous, small, with long cylindrical shafts not hollowed out at the base; anterior part of tongue retractile; palatines widely separate; T-shaped interclavicle; osteodermal plates absent from the body. *Xenosaurus* Ptrs., with one species, S. Mexico.

Fam. 8. **Zonuridae.** Pleurodont, teeth as in preceding, but hollowed out at the base; tongue short not retractile; supratemporal fossa roofed over by dermal ossifications; palatines and pterygoids widely separated, interclavicle cruciform; no abdominal ribs. *Zonurus* Merr., dermal ossifications on the trunk and tail, S. Afr. and Madagascar; *Pseudocordylus* Smith, S. Afr.; *Platysaurus* Smith, S. Afr.; *Chamaesaura* Schn., snake-like body and reduced limbs. S. Afr.

Fam. 9. **Anguidae.** Pleurodont, teeth solid at the base, new teeth originate between the old ones; teeth may be present on the pterygoids, palatines and vomers (*Ophisaurus*); anterior part of tongue emarginate, retractile into the posterior part; osteodermal plates on head and body; palatines and pterygoids well separated; limbs variously developed, may be absent, but limb-girdles always present; terrestrial; *Anguis* is viviparous; Amer., Eur., India. *Gerrhonotus* Wieg., 4 well-developed pentadactyle limbs, W. and S. N.-Amer., C. Amer.; *Ophisaurus* Daud. (*Pseudopus* Merr.), limbs absent, or reduced to vestiges of the hind pair, S.E. Eur., N. Afr., S.W. Asia, S. N.-Amer., Mexico; *O. apus* Pall., the glass-snake, Balkan Peninsula etc. *Diploglossus* Wieg., limbs pentadactyle, well developed, trop. Amer.; *Sauresia* Gr., limbs tetradactyle, W. Indies; *Panolopus* Cope, 4 limbs, anterior without digits, posterior with a rudimentary digit on the inner border, W. Indies; *Ophiodes* Wagl., no forelimbs

styliiform vestige of hind limbs, S. Amer.; *Anguis* L., teeth fang-like, no limbs, palate toothless, Eur., W. Asia, Algeria; *A. fragilis* L., slow-worm, blind-worm, eyes well developed with moveable lids, ear-opening minute, tail as long as body, to more than one ft.

Fam. 10. **Anniellidae.** Vermiform, limbs absent, eyes and ears concealed; tongue bifid; teeth large, fang-like, skull ophidian-like, no columella cranii, no squamosal, post-orbital arch ligamentous. *Anniella* Cope, California.

Fam. 11. **Helodermatidae.** Pleurodont, teeth fang-like and grooved with labial poison-glands; limbs well developed; tongue bifid; post-fronto-squamosal arch absent; osteoderms present. *Heloderma* Wieg., the poisonous lizard (Gila monster), Mexico; *Lanthanotus* Steind., Borneo is allied here.

Fam. 12. **Varanidae.** Pleurodont, old-world lizards with a long, bifid and protractile smooth tongue; osteoderms absent; postorbital arch incomplete; tail long; teeth large, dilated at the base. *Varanus* (*Hydrosaurus*) Merr., Monitor, with 30 species, Afr., S. Asia, Australia; in some species they attain to 7 feet.

Fam. 13. **Xantusiidae.** Pleurodont with short tongue, and supra-temporal fossa roofed by the cranial bones; no osteoderms; no moveable eyelids; C. Amer., and Cuba. *Lepidophyma* A. Dum., C. Amer.; *Xantusia* Baird, California; *Cricosaura* G. and P., Cuba.

Fam. 14. **Teliidae.** Dentition intermediate between pleurodont and acrodon, teeth not hollow at the base; tongue long and bifid, with scale-like papillae; palatines in contact anteriorly; no osteoderms; limbs various, they may be normal, or shortened (*Proctoporus*), or more reduced with incomplete number of digits (*Scolecossaurus*), or digits absent and as bud-like rudiments (*Cophias*, *Ophiognomon*, in one species of the latter the pelvic limbs are absent); confined to the New World, 40 genera, more than 100 species.

*Alopoglossus* Blgr., Ecuador, Peru; *Ameiva* Cuv., trop. Amer.; *Anadia* Gr., Costa Rica to Ecuador; *Argalia* Gr., Venezuela and Colombia; *Arthrosaura* Blgr., Ecuador; *Callopiastes* Gravl., Peru, Chili; *Centropyx* Spix, S. Amer.; *Cercosaura* Wagl., Brazil; *Cnemidophorus* Wagl., Amer.; *Cophias* Fitz., S. Amer.; *Crocodylurus* Spix, Guianas, Brazil; *Dicrodon* D. and B., Peru; *Dracaena* Daud., Guianas and Amazon; *Eclipseopus* D. and B., S. Amer.; *Euspondylus* Tsch., Venezuela to Peru; *Gymnophthalmus* Merr., trop. Amer.; *Heterodactylus* Spix, Brazil; *Iphisa* Gr., Brazil, Guianas; *Leposoma* Spix, S. Amer.; *Loxopholis* Cope, Colombia; *Micrablepharus* Boettg., Brazil, Paraguay; *Monoplocus* Gthr., trop. Amer.; *Neusticurus* D. and B., S. Amer.; *Ophiognomon* Cope, Upper Amazons; *Oreosaurus* Ptrs., Colombia, Ecuador, Brazil; *Pantodactylus* D. and B., S.E. S. Amer.; *Perodactylus* R. and L. Brazil; *Pholidobolus* Ptrs., Ecuador; *Placosoma* Tsch., Brazil; *Prionodactylus* O'Sh., S. Amer.; *Proctoporus* Tsch., Andes of Ecuador and Peru; *Scolecossaurus* Blgr., S. Amer.; *Teius* Merr., S.E. S.-Amer.; *Tupinambis* Daud., teju, to 3 ft., S. Amer.; *Tretioscincus* Cope, Colombia, C. Amer.

Fam. 15. **Amphisbaenidae.** Vermiform, teeth acrodon or pleurodont, scales of body reduced, skin soft divided into squarish segments forming regular annuli; eyes and ears concealed; limbs absent, except in *Chirotres*, which has 4-clawed forelimbs; girdles much reduced; sternum absent except in *Chirotres* in which it is not connected with the ribs; tail short; skull without interorbital septum, epipterygoid, postorbital and fronto-



squamosal arches ; antero-lateral walls of skull completely closed by bone as in *Ophidia* ; burrowers, may live in ant's nests and manure heaps, can progress backwards, and forwards in their burrows by slight vertical undulations ; Amer., W. Indies, Africa and round Mediterranean. *Chirotos* Cuv., Mexico, California, Platte River ; *Blanus* Wagl., borders of Mediterranean ; *Amphisbaena* L. (Fig. 193), trop. Amer. and Afr. ; *Anops* Bell, S.E. S.-Amer., W. Afr. ; *Geocalamus* E. Afr. ; *Monopeltis* Smith, Afr. ; *Rhineura* Cope, Florida ; *Lepidosternon* Wagl., S. Amer. ; *Trogonophis* Kaup, N.-W. Afr. *Pachycalamus* Gthr., Socotra ; *Agamodon* Ptrs., E. Afr.

Fam. 16. **Lacertidae.** Pleurodont ; tongue long, bifid, with papillae or folds ; pterygoid often with teeth ; pterygoids and palatines separate mesially ; postorbital and postfronto-temporal arches complete, temporal fossa roofed over by large postfrontals and by osteoderms ; no osteoderms on body ; limbs well developed, pentadactyle ; tail long, brittle ; some genera have a transparent patch in the lower eyelid, so that they can see when the eye is shut (*Eremias*, *Cabrita* etc.), and in *Ophiops* the lower eyelid is fused with the upper ; about 20 genera and 100 species, Old World, but not in Madagascar or Australia. *Acanthodactylus* Wieg., S. Spain and Portugal, Afr. n. of eq., S.W. Asia ; *Algiroides* Bibr., E. coast of Adriatic, Greece, Sardinia, Corsica ; *Aporosaura* Blgr., W. Afr. ; *Cabrita*, Gr., India ; *Eremias* Wieg., Afr., Asia ; *Gastropholis* Fisch., E. Afr. ; *Holaspis* Gr., W. Afr. ; *Ichnotropis* Ptrs., Afr. s. of eq. *Lacerta* L., Eur., N. and W. Asia, Afr. north of equator, *L. vivipara* Jacq. the common English Lizard, the only reptile found in Ireland ; the young are hatched in the uterus or directly after the eggs are laid ; *L. agilis* L. sand lizard, also found in S. of England ; *L. viridis* Laur., found in Jersey ; *L. ocellata* Daud. the eyed-Lizard, S. France, N.W. of Italy, Spain, Portugal ; *L. muralis* Laur., S. Eur., N. Afr., Asia Minor. *Latastia* Bedr., E. Afr., Arabia ; *Nucras* Gr., trop. and S. Afr. ; *Ophiops* Mén., Turkey, N.-Afr., Asia ; *Poromera* Blgr., W. Afr. ; *Psammadromus* Fitz., S.W. Eur., N. Afr. ; *Scapteira* Wieg., C. Asia, S. Afr. ; *Tachydromus* Daud., E. Asia, Japan, Ind. Archipelago ; *Tropidosaura* Fitz., S. Afr.

Fam. 17. **Gerrhosauridae.** Pleurodont, with osteoderms on head and body ; limbs sometimes reduced ; Africa S. of Sahara, and Madagascar. *Gerrhosaurus* Wieg., *Tetradactylus* Merr., *Cordylosaurus* Gr., *Zonosaurus* Blgr., Madagascar ; *Tracheloptychus* Ptrs., Madagascar.

Fam. 18. **Scincidae.** Pleurodont, with strongly developed osteoderms on head and body ; tongue scaly, feebly nicked ; premaxillaries sometimes separated ; cranial arches complete ; limbs may be reduced or absent, but this feature is not an indication of affinity within the family, there may be a transparent disc on the lower eyelid ; all are viviparous ; nearly 30 genera, and 400 species, cosmopolitan including Pacific Islands.



FIG. 193.—*Amphisbaena fuliginosa* (Règne animal).



*Ablepharus* Fitz., lower eyelid fused with upper, Australia, S.W. Asia, S.E. Eur., trop. and S. Afr.; *Acontias* Cuv., S. Afr., Madagascar, Ceylon; *Brachymeles* D. and B., Phillipines; *Chalcides* Laur. (*Seps*), S. Eur., N. Afr., S.W. Asia; *Chalcidoseps* Blgr., Ceylon; *Corucia* Gr., Solomon Islands; *Egernia* Gr., Australia; *Eumeces* Wieg., N. and C. Amer., E. and S.W. Asia, N. Afr.; *Hemisphaeriodon* Ptrs., Queensland; *Herpetoseps* Blgr., S. Afr.; *Lygosoma* Gr., 160 species, Australasia, E. Indies, China, N. and C. Amer., trop. and S. Afr.; *Mabuia* Fitz., semiaquatic, 70 species, Afr., Madagascar, S. Asia, C. and S. Amer., W. Indies; *Macroscincus* Bocage, Cape Verde Islands; *Melanoseps* Blgr., E. Afr.; *Ophiomorus* D. and B., Greece, Asia Minor to Syria; *Pygomeles* Grand., Madagascar; *Ristella* Gr., India; *Scelotes* Fitz., trop. and S. Afr. Madagascar; *Scincus* Laur., (Fig. 194) N. Afr., Arabia, Persia, Scind; *Sepophis* Bedd., S. India; *Sepsina* Boc., S. Afr., Madagascar; *Tiliqua* Gr. (*Cyclodus*), stout lateral teeth with spherical crowns, Australia, Austo-Malay and Indo-Malay; *Trachysaurus* Gr., Australia; *Tribolonotus* D. and B., New Guinea; *Tropidophorus* D. and B., S. China, Indo-China, Phillipines, Borneo; *Typhlacontias* Boc., S.W. Afr.

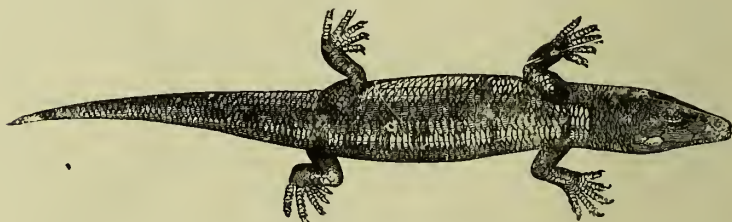


FIG. 194.—*Scincus officinalis* (Règne animal).

Fam. 19. **Anelytropidae.** Degraded Scincoids, burrowing, limbless, with osteoderms; without bony postorbital and postfrontosquamosal arches; interorbital septum and columella cranii well developed, with abdominal ribs; eyes concealed, no ear opening; trop. and S. Afr., Mexico. *Anelytropis* Cope, Mexico; *Feylinia* Gr., W. Afr.; *Typhlosaurus* Wieg., S. Afr.

Fam. 20. **Dibamidae.** Body vermiform; tongue pointed, undivided in front; no interorbital septum or columella cranii; no cranial arches; limbs absent, no sternum, eyes concealed, no ear opening. *Dibamus* D. and B., New Guinea, Moluccas, Nicobars.

*Ophiopsiseps* Blgr., Australia is probably the type of a distinct family; snake-like; eyes without lids, scaly tongue; Australia.

Sub-order 2. **Rhiptoglossa.** Nasal bones not bounding nasal apertures; pterygoid not reaching quadrate; clavicles and interclavicle absent, limbs well developed; tongue vermiform, projectile.

Fam. 21. **Chamaeleontidae.** Acrodont, teeth on the maxillaries and mandible; premaxillaries and palate without teeth; tongue projectile to

a length equal to that of the body, club-shaped and viscose at the end ; digits arranged in two bundles of two and three respectively ; eyes large covered with a thick granular lid pierced by a small central opening for the pupil ; they act independently of one another. Tympanum and tympanic cavity absent ; skin with great power of changing colour ; \* skull with interorbital septum, without columella cranii (epipterygoid) ; parietal single forming a crest and meeting posteriorly the supra-temporals which connect it on each side with the squamosals ; parietal not moveable upon occipital ; nasals narrow, not entering nasal apertures ; pterygoids do not reach quadrate ; quadrate not moveable ; vertebrae procoelous ; abdominal ribs present ; the tail is prehensile, coiling ventralwards, not renewable ; the lungs end in several diverticula which extend far back into the body cavity ; a few species are viviparous ; about 50 species, most in Afr., Madagascar, a species in Socotra, another in S. Arabia, and a third in India and Ceylon. *Chamaelcon* Laur., Afr., Madagascar, S. of Spain, Arabia, India, Ceylon ; *Ch. vulgaris*, Daud., N. Afr., Syria, Asia Minor, Andalusia, to one ft. ; *Ch. pumilus* Daud., to 5 or 6 in., S. Afr. : *Ch. parsoni* Cuv., to two ft., Madagascar ; *Brookesia* Gr., Madagascar ; *Rhampholeon* Gthr., trop. Afr.

#### Order 4. OPHIDIA. †

*Elongated Reptiles without limbs, with horny epidermal scales without osteoderms, with moveable quadrate bones, transverse anal opening, and paired copulatory organs. Without eyelids, tympanic cavity, urinary bladder and sacrum. The rami of the mandible are united at the symphysis by an elastic ligament.*

Snakes are chiefly characterised by the absence of extremities, and by the distensibility, which is sometimes extraordinary, of the mouth and pharynx. They cannot however be sharply separated from lizards. Formerly the limitations of this class rested entirely upon the absence of limbs, and thus not only were the *Gymnophiona* among the *Amphibia*, but also the blind worms and other genera of apodal lizards included in it. Moreover some snakes have traces of posterior limbs which are placed at the root of the tail and carry a conical claw projecting at the sides of the anus.

\* Thilenius, *Morphol. Arbeiten*, 7, 1897, p. 515 ; Keller, *Arch. Physiol.*, 61, 1895, p. 123.

† J. Müller, "Ueb. eine eigenthümliche Bewaffnung des Zwischenkiefers der reifen Embryonen der Schlangen u. Eidechsen," *Müller's Arch.*, 1841. Duméril et Bibron, "*Erpetologie générale*," Paris, 1854. A. Günther, "On the geographical distribution of Snakes," *Proc. Zool. Soc.*, 1858. Id. "*The Reptiles of British India*," London, Ray Society, 1864. G. Jan, "*Iconographie générale des Ophidiens*," Paris, 1860-82. Lenz, "*Schlangenkunde*," ed. 2, Gotha, 1870. G. L. Boulenger, "*Catalogue of Snakes in the British Museum*," London, 1893-6. Huxley, Cope, Zittel, Gadow, *op. cit.*

The skin is scaly, but the scales are purely epidermal structures placed on thickenings of the cutis; osteoderms are absent. The scales vary much in form, number and arrangement. When they are small and overlap they are called scales, but when they are large and only touch by their edges the term shield is applied to them.

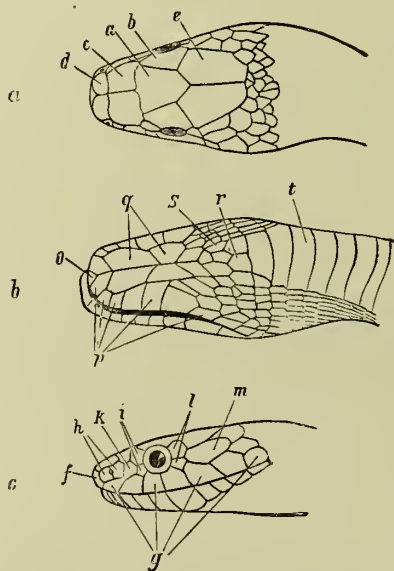


FIG. 195.—Head of *Calopeltis aesculapii*. *a* dorsal, *b* ventral view. *c* side view of head of *Tropidonotus viperinus* (from Claus, after E. Schreiber). *a* frontal shield; *b* superciliary shields; *c* posterior snout, *d* anterior snout, *e* parietal, *f* rostral shield; *g* upper labial shields; *h* nasal shield; *i* preorbital shield; *k* loreal, *l* postorbital, *m* temporal, *o* median labial shield; *p* lower labial shields; *q* mental shields; *r* jugular shields, *s* jugular scales; *t* ventral shields.

The scales of the head are distinguished according to their position (Fig. 195). The mental shields (*q*), i.e. the scales in the mental groove on the ventral surface between the rami of the lower jaw, may be mentioned as peculiar to snakes; in front of these two accessory labial shields on either side form with the median labial shield (*o*) the anterior boundary of the mental groove. The scales on the ventral surface are for the most part broad and invest the body like transverse bands (Fig. 195 *b*, *t*), but small scales may also be present here. The ventral surface of the tail, on the other hand, is as a rule, covered by a double, or rarely by a single, row of shields.

Snakes moult several times in the course of the year. They strip off the whole of the scaly epidermis.

The vertebrae are very numerous and are divided into caudal and precaudal

only. All the precaudal vertebrae, except the atlas, carry ribs, and the caudal vertebrae have long transverse processes. The vertebrae are procoelous, the posterior surfaces being hemispherical. The zygapophyses are flat and look dorsally and ventrally and in addition to them the anterior side of the neural arch carries above the neural canal a wedge-like process—the zygosphenes (Fig. 196) which fits into a corresponding depression—the zygantrum—on the posterior surface of the

neural arch of the preceding vertebra. The neural arches are completely fused with the centra. The transverse processes in the trunk are short and carry the ribs. Some of the anterior trunk vertebrae have hypapophyses. In *Dasypeltis* the anterior of these are tipped with an enamel-like substance (p. 368). There are no chevron bones, but the transverse processes of the caudal vertebrae have strong descending processes which have the same relation to the caudal vessels. The atlas and axis are similar to those of lizards. The vertebral column is capable of a considerable amount of lateral flexion, but of very little, if any, dorso-ventral flexion.

The ribs are articulated to the transverse processes of the trunk

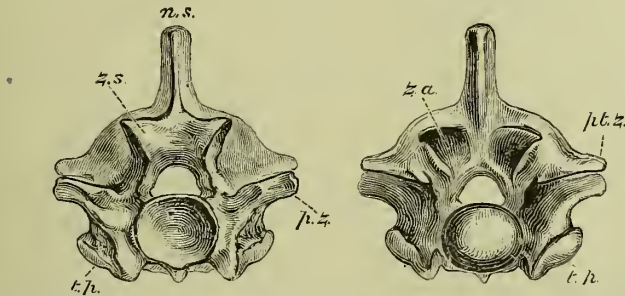


FIG. 196.—Anterior and posterior view of a trunk vertebra of a Python (from Huxley), *zs* zygosphenes; *z a* zygantrum; *p z* prezygapophysis; *p t z* postzygapophysis; *t p* transverse process.

vertebrae. They have capitula only, and are very moveable in an antero-posterior direction. They are usually hollow and end ventrally in a cartilage which is attached to the connective tissue underlying the ventral shields. The movements of the ribs in combination with the flexion of the vertebral column are of great use in locomotion. Snakes run, in a sense, on the extreme points of their ribs which are moved forwards, carrying with them the ventral shields to which they are attached. There is no trace of a sternum in any snake.

The skull presents a number of peculiarities in which it differs from the ordinary lacertilian type; but it is interesting to notice that some of these crop up in different families of lizards. The most important points of difference are the following. (1) The cranial cavity is long and extends, but little diminished in depth, into the interorbital region, there being no interorbital septum.



The anterior and middle parts of its walls are formed by descending processes of the parietal and frontal bones (Fig. 197 *B*), and there is no epipterygoid (columella). The bones of the cranium are firmly and suturally connected and there are no membranous fontanelles; in these points it resembles the *Amphisbaenidae*. (2) There are no parotic processes. (3) The basisphenoid is continued forwards as an ossified rostrum (Fig. 197 *B*), which probably represents a parasphenoid element, into the ethmoidal region. (4) The nasal region is but slightly ossified, and the

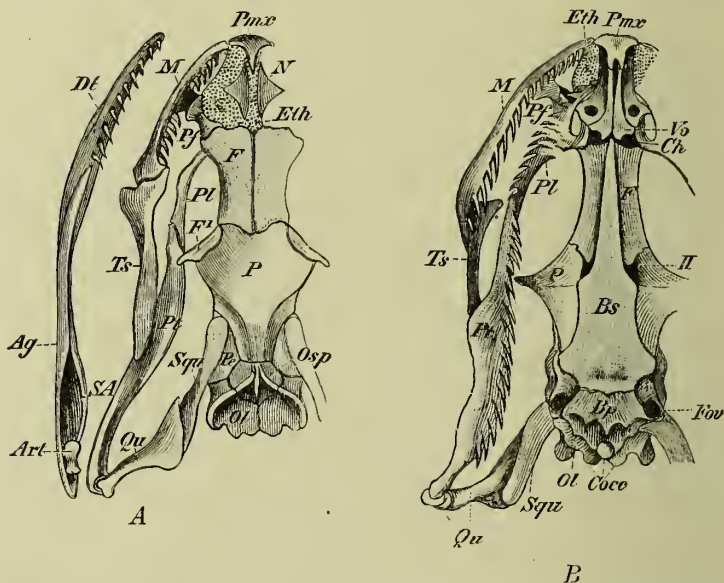


FIG 197.—Skull of *Tropidonotus natrix*. A dorsal, B ventral view (from Wiedersheim). Ag angular, Art articular; Bp basioccipital; Bs basisphenoid; Ch choanae; Coc occipital condyle; Dt dentary; Eth ethmoid; F frontal; Fu foramen for optic nerve; M maxilla; N nasal; Ol exoccipital; Ool supraoccipital; P parietal; Pe periotic; Pf prefrontal; Pl palatine; Pmx premaxilla; Pt pterygoid; Qu quadrate; SA surangular; Squ squamosal; Ts transpalatine; Vo vomer.

premaxilla is small, unpaired, and only connected with the maxilla by ligament. (5) The temporal arcades are absent: the postfrontal is not directly connected with the squamosal, and there is no jugal or quadrato-jugal; the geckos and amphisbaenids among lizards present approximations in these respects. (6) The palatines do not unite directly with the vomers or with the base of the skull. They are joined behind to the pterygoids, which are connected with the maxillae by long transpalatine



bones and posteriorly with the highly mobile quadrates. (7) There is no parietal foramen. (8) The rami of the lower jaw are not united at the symphysis but connected only by an elastic ligament.

The supraoccipital does not enter into the foramen magnum (Fig. 197 *A*, *Osp*). The parietal is unpaired and sends down lateral processes which articulate with the basisphenoid. The frontals are paired and send down lateral processes which unite with one another on the floor of the skull dorsal to the basisphenoidal rostrum. This is a unique arrangement.

Whether these downward processes contain elements of the orbitosphenoid and alisphenoid is not clear. According to Rathke \* the parietals and frontals arise from paired centres of ossification in patches of cartilage in the dorso-lateral part of the skull. That there is something unusual in this part of the skull is further rendered probable by the fact that the trabeculae crani persist in many adult snakes as two separate cartilaginous rods placed in grooves on the dorsal side of the basisphenoidal rostrum and ventral to the union of the frontals.

There are postfrontals behind the orbit, and prefrontals lying upon the ethmoid cartilage in front of the orbit (Fig. 197 *A*, *F'*, *Pf*). The prefrontals have descending processes for articulation with the maxillae and palatines. There are two nasals and two vomers (*vo*) close together and in front of the choanae (*Ch*). The quadrates are very moveably articulated to the posterior end of the squamosals, which are elongated and project back from the parietal region of the skull (Fig. 197, *Qu*).

The lower jaw contains the usual bones but the coronoid is sometimes absent. The hyoid is much reduced, consisting of a pair of cartilaginous rods lying ventral to the trachea and united in front.

In the *Typhlopidae* the palatines are placed transversely and meet in the middle line. The pterygoids are not joined to the quadrates and there is no transpalatine. In *Xenopeltis*, which like *Python* has teeth in the premaxilla, the squamosal is applied to the side wall of the skull, so that the short quadrate appears to articulate directly with the skull. In most non-poisonous snakes a row of recurved teeth is present on the maxillae, palatines and pterygoids, the palatine and pterygoid are arranged longitudinally and are firmly connected, and the squamosals are slightly moveable. In the *Viperidae* the maxillae are short and moveably articulated with the prefrontal. The squamosal, and quadrate are very moveable and the pterygoid is moveably attached to the palatine. The maxillae each possess only one large tooth—the poison fang—which contains a

\* *Ueb. d. Entwicklungsgesch. der Natter*, Königsberg, 1839.

canal open at each end. The poison gland opens at the base of the fang and its secretion passes into the canal. When the mouth is shut, the fangs are directed backwards and lie along the roof of the mouth. When the mouth opens (Fig. 198) the ventral end of the quadrate, which when at rest is inclined backwards, is brought forward. The pterygoid is thus thrust forward and the pterygo-palatine joint bent. This forward movement of the pterygoid is conveyed by the transpalatine bone to the maxilla and causes it to rotate through about  $90^\circ$  upon its prefrontal articulation, in such a way that the surface to which the fang is attached is carried forwards and ventralwards, and the fang is erected, i.e. is made to project downwards at the front end of the mouth (Fig. 198).

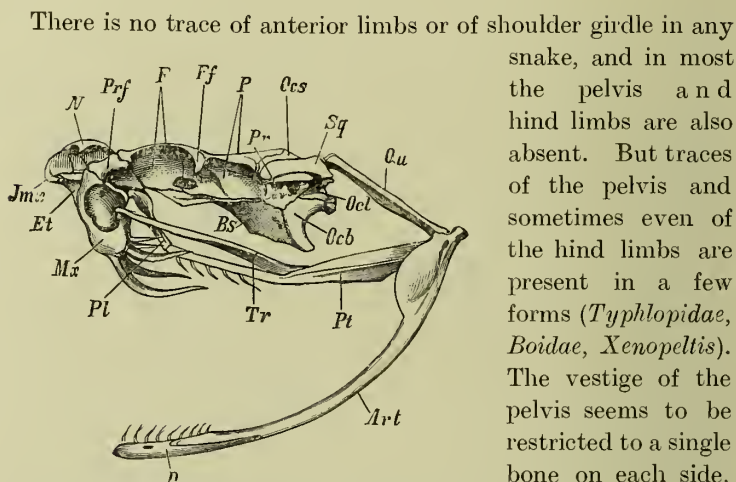


Fig 198.—Skull of *Crotalus horridus* (from Claus). *Art* articular; *Bs* basisphenoid; *D* dentary; *Et* ethmoid; *F* frontal; *Jmx* premaxilla; *Mx* maxillary; *N* nasal; *Ocb* basioccipital; *Ocl* exoccipital; *Ocs* supraoccipital; *P* parietal; *Pf* postfrontal; *Pr* prootic; *Pl* palatine; *Prf* prefrontal; *Pt* pterygoid; *Qu* quadrate; *Sq* squamosal; *Tr* transpalatine.

snake, and in most the pelvis and hind limbs are also absent. But traces of the pelvis and sometimes even of the hind limbs are present in a few forms (*Typhlopidae*, *Boidae*, *Xenopeltis*). The vestige of the pelvis seems to be restricted to a single bone on each side, longitudinally disposed and embedded in the muscle near the anus; it is

probably the ischium. To these, very short vestiges of hind limbs carrying claws are frequently attached.

**Alimentary Canal.** The teeth are acrodont and ankylosed to the jaws. They are sharp-pointed and curved backwards. They are usually absent from the premaxillae, but are present on the maxillae, palatines, and pterygoids (occasionally absent from the pterygoids) and on the dentaries. They chiefly serve to hold the prey while it is being swallowed. In most of the non-poisonous snakes the teeth are conical, but in the others and in all the poisonous forms some of the maxillary teeth are grooved in front. This groove is in the most poisonous forms

(*Viperidae*) converted into a canal open at both ends. The teeth appear to be continually replaced.

Labial glands are present in a row in the upper and lower jaw. The posterior labial gland of the upper jaw is in the poisonous snakes modified as the poison gland. It is larger than the rest and different in structure, and its duct opens into the mouth, sometimes at the base of the poison fang (*Viperidae*). Sublingual glands in the floor of the mouth are also present.

The tongue is long, narrow and forked, and retractile into a basal sheath. It is well provided with sense organs and is exceedingly protractile. It is used as a tactile organ, and can be protruded through an indentation at the extremity of the snout even when the mouth is closed; eustachian tubes and tympanic cavities are absent. The glottis is placed far forwards, close behind or even perforating the tongue-sheath, and can be projected into the mouth during the act of swallowing. The oesophagus is long and leads into the tubular stomach, the anterior part of which is dilated, the posterior (pyloric) narrow and intestine-like. The windings of the small intestine are connected together by connective tissue and enclosed in a common sheath of peritoneum. The rectum varies in length and there may be a caecum on the anterior part of it. The liver is elongated and not divided into lobes: it extends from the pericardium to the cardiac region of the stomach. The gall-bladder is placed at some distance from it, on the right side of the duodenum. The pancreas lies on the right side of the duodenum, into which it opens by one or more ducts close to or in common with the bileduct. The spleen is usually distinguished by its light colour and is placed near the pancreas.

The cloaca is without a urinary bladder. The anus is placed at the junction of the body and tail, which varies in length in the different families.

Fat-bodies are present in the form of lobed structures on each side of the intestine in the hinder part of the body-cavity.

Thymus and thyroid are present, and the suprarenal bodies have the form of narrow elongated bodies of a yellow colour placed on the renal veins or on the vena cava inferior.

The glottis is a longitudinal slit and is without distinct epiglottis, though there may be a trace of the latter. The larynx consists of two lateral longitudinal cartilages connected ventrally

and sometimes dorsally by transverse pieces. There are no vocal cords. The trachea is long and the tracheal rings are complete in front, incomplete behind. The lungs are saccular and provided with air-cells in their walls. They are never symmetrical. As a rule the left is the smaller, and in some cases, e.g. most poisonous snakes, one lung is completely suppressed. In such cases the posterior end of the trachea may possess, usually on its dorsal side, air-cells in its walls and take on the structure of a lung. In many snakes the alveolar structure is less marked and may be entirely absent in the hind end of the lung. It thus happens that in these snakes, as in some lizards (*Chamaeleo*), the hind end of the lung has a smooth wall without lung structure and is supplied with blood vessels from the systemic circulation. Inspiration is effected by swallowing movements as in *Amphibia* and lizards.

The **brain** is very similar to that of lizards, but there is no parietal organ. The spinal accessory cranial nerve is not present, and the sympathetic system is but feebly developed, the viscera in the greater part of the trunk being supplied by the ventral rami of the spinal nerves.

The eyelids are always fused over the eye, so that the conjunctival space is closed and there appear to be no eyelids (see p. 317). The lacrymal gland opens into this space, which also communicates with the nose by a lacrymal canal. There is no retractor bulbi muscle.

Tympanic membrane, tympanic cavity and eustachian tube are absent. In spite of this snakes appear to have a good sense of hearing. The columella auris extends from the stapedial plate to the quadrate, against which it abuts by a cartilaginous epiphysis. In some snakes the stapes is a bony plate closing the fenestra ovalis and without a shaft-like columella.

The nasal openings are usually placed at the front end of the snout.

The **heart** is placed far back at some distance from the head. It is constructed as in lizards and chelonians. There are a sinus venosus, two auricles, and a single ventricle imperfectly divided by a septum. Three arteries leave the ventricle, the pulmonary artery and two systemic arches. The right systemic arch gives off the single or double carotid artery. In many snakes (*Python*, *Boa*, *Tropidonotus*, *Xenopeltis*, etc.) there are two

carotids.\* These may arise from the arch by a common stem, and the right is usually smaller than the left. In other snakes only one carotid and that the left is present. In such cases it often happens that there is an artery in place of the right carotid, which goes to the blood-glands in front of the pericardium (*a. thyroidea*). There are, of course, no subclavians. The left arch gives off no vessels. The anterior abdominal vein is single and arranged as in *Lacertilia*, i.e. it conveys blood from the ventral body wall and bladder to the liver. The caudal vein is continued as the renal portal.

The **kidneys** are elongated, slightly lobed bodies placed at some little distance in front of the cloaca. They are not quite symmetrical the right extending a little further forward than the left. The ureters leave their hind ends and are of some length; they open through the side-walls of the cloaca on a papilla which in the males contains also the opening of the vas deferens. There is no urinary bladder.

The **genital glands** are like the kidneys slightly asymmetrical; those of the right side reaching a little further forward than the left. The testes are usually rather elongated bodies and lie in front of the kidneys. The coiled vasa deferentia lie along their inner sides and open behind, as stated, into the cloaca close to the ureters. The ovaries are elongated and consist of two lamellae with a lymph space between them. The oviducts have the usual arrangement. The penes are paired evaginable cloacal pouches and closely resemble those of lizards.

Accessory glands in the neighbourhood of the anus are found in both sexes of many snakes.

Most snakes are oviparous, but in a few (many sea-snakes and vipers) the development takes place in the oviduct and the young are born fully developed. The eggs have soft shells and are laid in comparatively small numbers, it may be at an advanced stage of development. The embryo possesses a tooth-like process on its premaxilla for breaking the shell.

Snakes feed exclusively on living animals, both warm and cold-blooded, which they attack suddenly, and swallow without mastication. Swallowing is effected thus: the teeth on the lower jaw are alternately hooked further and further forwards into the body of the prey (the two halves of the mandible

\* Rathke, *Denkschriften Wiener Akad.* xi, 1856, Abt. 2, p. 1.



moving forwards alternately), as a result of which the mouth and pharynx of the snake are gradually drawn over the animal, the surface of which is at the same time made slippery by the secretion of the buccal glands. During this process the larynx is projected forwards between the rami of the jaws, so that respiration can be maintained. After the completion of the laborious process of swallowing, the animal appears to be entirely prostrated and passes a long period in inactivity, during which the slow digestion takes place.

Some snakes kill their prey by crushing, e.g. Python; some by poison; and others, the majority, swallow their prey directly. The poisonous snakes belong to different families and cannot easily be distinguished by any external mark from the non-poisonous. The poison is secreted by some of the upper labial glands, and is introduced into the subcutaneous tissue of the victim by a groove (in the *Viperidae* converted into a canal) on the anterior side of some of the maxillary teeth

The actual poison of the venom appears to consist of albuminous substances in solution, and is different, judging by its action, in different snakes.\* The best treatment is to inject the serum of animals which have been rendered partially immune by repeated doses of the venom. Failing this, the best plan is to apply a ligature above the wound, twisting the string with a stick, and then to make a free incision of the wound. "Then bandage the limb downwards towards the wound, repeating this several times. Direct application into the widened wound of bleaching powder (calcium hypochlorite) or of a 1 per cent. solution of Condyl's fluid is good. Amputation is of course the best remedy, if a very deadly snake has bitten the part." Alcohol and injection of ammonia are useless, and sucking the wound is dangerous. Many mammals are said to be immune to snake-venom, e.g. the mongoose, the hedgehog and the pig.

Most of the species distinguished by size or beauty of colour belong to the warmer zones, only the smaller forms extend into northern temperate climates. Many snakes are fond of the water and are truly amphibious. Others live for the most part on trees or shrubs, or on sandy ground; others exclusively in the sea. In temperate climates they fall into a kind of winter sleep; in hot countries they may undergo a summer sleep in the dry season.

About 400 genera and 1,800 species are known. Very few fossil forms are known. It is claimed that they make their first

\* See Martin in Allbutt's *System of Medicine*, 2, London, 1896.

appearance in the Cretaceous, but this is doubtful. Fragments are however found in the Eocene (*Palaeophis*, etc.), and the remains become more extensive<sup>as</sup> the present time is approached.

**Fam. 1. Typhlopidae.** Burrowing snakes with reduced eyes covered by the scales, and without teeth in the lower jaw ; maxilla transversely placed and toothed, palate toothless. The cranial bones are solidly united ; there are no ectopterygoids or squamosals (supratemporal) and the pterygoids are not united to the quadrates ; vestiges of the pelvis as a single bone on each side ; widely distributed, absent from New Zealand. *Helminthophis* Ptrs., trop. Amer. ; *Typhlops* Schn. (Fig. 199), S. Eur., S. Asia, Afr., trop. Amer., Australia, about 110 species ; *Typhlophis* Ptrs., Brazil and Guiana.

**Fam. 2. Glauconiidae.** Like the former, but maxillaries normal and toothless, lower jaw toothed. The pelvic girdle and hind limbs show the least reduction in any snake ; the ilium, pubis and ischium can be distinguished, the latter forming a symphysis, and there is a vestige of a femur. *Anomalepis* Jan, Mexico ; *Glauconia* Gr., Africa, S.W. Asia., Amer., 30 species.

**Fam. 3. Boidae.** Usually large snakes with vestiges of the hind limbs appearing as spurs on each side of the anus ; the ventral scales are transversely enlarged and the eyes are functional and free. Teeth are present on the mandibles, pterygoids, palatines, maxillaries and in some genera on the premaxillaries. Maxilla, palatine, pterygoid moveable ; ectopterygoid present and pterygoid extending to quadrate ; squamosal present, suspending quadrate ; prefrontal in contact with nasal ; vestiges of pelvis and hind limbs present ; worldwide except New Zealand ; prefer wooded districts, climbing trees ; crush their prey in the coils of the body ; oviparous ; 20 genera.

*Aspidites* Ptrs., N. Australia ; *Boa* L., trop. Amer., Madagascar ; *B. constrictor* L., S. Amer., to 11 ft. ; *Bolieria* Gr., Round Island near Mauritius ; *Calabaria* Gr., W. Afr. ; *Casarea* Gr., Round Island near Mauritius ; *Charina* Gr., W. N.-Amer. ; *Chondropython* Meyer, New Guinea ; *Corallus* Daud., trop. Amer., Madagascar ; *Enygrus* Wagl., Moluccas, Papuasias, Polynesia ; *Epicrates* Wagl., trop. Amer. ; *Eryc* Daud., N. and E. Afr., S. and C. Asia ; *Eunectes* Wagl., the anaconda, aquatic and arboreal in habit, S. Amer. ; *Liasis* Gr., Flores, Timor, Papuasias, N. Australia ; *Lichanura* Cope, California ; *Loxocemus* Cope, Mexico ; *Nardoa* Gr., New Zealand ; *Python* Daud., trop. and S. Afr., S.E. Asia, Papuasias, Australia ; *P. spilotes* Lacép., the carpet-snake, N. Guinea, Australia ; *P. reticulatus* Schn., Indo-China, Malay Isl., to

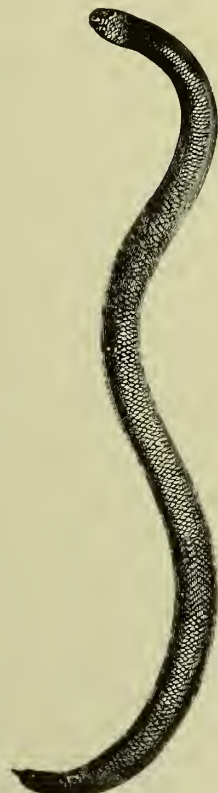


FIG. 199.—*Typhlops tumbrioides* (Règne Animal).

30 ft.; *P. molurus* L., India and Ceylon, to 30 ft.; *Trachyboa* Ptrs., S. Amer.; *Ungalia* Gr., W. Indies, Guatemala, Ecuador, Peru; *Ungaliophis* F. Müll., Guatemala.

Fam. 4. **Ilysiidae**. Cranial bones are more or less solidly united; ventral scales hardly enlarged; teeth and pelvis as in the last. *Ilysia* Hemp., S. Amer.; *Anomalochilus* Jeude, Sumatra; *Cylindrophis* Wagl., Ceylon and S.-E. Asia.

Fam. 5. **Uropeltidae**. Burrowing snakes of small size, restricted to Ceylon and S. India. Cranial bones solidly united, pterygoid not reaching quadrate, with ectopterygoid, without squamosal; eye small; tail short ending in a large shield. *Uropeltis* Cuv., Ceylon; *Rhinophis* Hemp., Ceylon and S. India; *Silybura* Ptrs., India, Ceylon; *Pseudoplectrurus* Blgr., S. India; *Plectrurus* S. India; *Melanophidium* Gthr., S. India; *Platyplectrurus* Gthr., S. India.

Fam. 6. **Xenopeltidae**. Cranial bones more or less solidly united; ectopterygoid present, pterygoid reaching quadrate, squamosal present, prefrontal in contact with nasal; teeth in jaws, palate and premaxillary; mandible without coronoid; dentary moveably articulated to the articular; tail short; a single genus and species *Xenopeltus* (Tortrix) *unicolor* Reinw., in S.-E. Asia.

Fam. 7. **Colubridae**. Facial bones moveable, prefrontal not in contact with nasal, ectopterygoid present, pterygoid extending to mandible or quadrate, squamosal present, maxillaries horizontal, mandible without coronoid, both jaws and palate toothed; 242 genera, cosmopolitan, with terrestrial, arboreal and aquatic forms. The family is divided into 3 series. Series A. AGLYPHA.—All the teeth solid, not grooved. Series B. OPISTHOGLYPHA.—One or more of the posterior maxillary teeth grooved. Series C. PROTEROGLYPHA.—Anterior maxillary teeth grooved or perforated.

#### Series A. AGLYPHA.

The Aglypha are harmless non-poisonous snakes and are divided into 3 subfamilies.

Sub-fam. 1. **Acrochordinae**. The postfrontal bone produced over the supraorbital region; scales not or but slightly imbricate; S.-E. Asia and C. Amer.; many species are aquatic in rivers and estuaries. *Acrochordus* Hornst., Malay P. and Arch., N. Guinea; *Xenodermus* Reinh., Java, Sumatra, Penang; *Chersydrus* Cuv., mouths of rivers and coasts of S.-E. Asia and Papuasia; *Stoliczkaia* Jerd., Khasi Hills, N.-E. India; *Nothopsis* Cope, C. Amer.

Sub-fam. 2. **Colubrinae**. Postfrontal bones not produced over the supraorbital region; scales usually imbricate; teeth on the entire length of the maxillary and dentary bones; cosmopolitan, but scarce in Australia. The sub-family contains about 1,000 species, and the genera may be arranged in two groups according to the presence or absence of hypapophyses on the posterior dorsal vertebrae.

I. Genera which have the hypapophysis on all the vertebrae, arranged alphabetically.

*Ablabophis* Blgr., S. Afr.; *Achalinus* Ptrs., China, Japan; *Amphiardis* Cope, Texas; *Aspidura* Wagl., Ceylon; *Blythia* Theo., Khasi Hills; *Boodon* Gthr., trop. and S. Afr.; *Bothrolycus* Gthr., W. Afr.; *Bothrophthalmus* Ptrs., trop. Afr.; *Brachyorrhus* Boie, Malay Arch., N. Guinea; *Chersodromus* Reinh., Mexico and Guatemala; *Cyclocorus* D. and B., Philippines; *Compsophis* Mocq., Mad.;

*Dromicordryas* Blgr., Mad. ; *Elapoides* Boie, Malay Arch. ; *Glypholycus* Gthr., C. Afr. ; *Goniontophis* Blgr., Congo ; *Haldea* B. and G., N. Am. ; *Haplocercus* Gthr., Ceylon ; *Helicops*, Wagl., C. and S. Amer., S.-E. As., trop. Afr. ; *Hormonotus* Hallow, W. Afr. ; *Hydraethiops* Gthr., trop. Afr. ; *Hydrablades* Blgr., Borneo ; *Ischognathus* D. and B., N. and C. Am. ; *Lamprophis* Smith, S. Afr. ; *Lioheterodon* D. and B., Mad. ; *Liophidium* Blgr., Madagascar ; *Lycognathophis* Blgr., Seychelles ; *Lycophidium* D. and B., trop. and S. Afr. ; *Macropisthodon* Blgr., E. Indies ; *Micropisthodon* Mocq., Mad. ; *Opisthotropis* Gthr., W. Afr., S. China, Malay Arch. ; *Oxyrhabdium* Blgr., Philippines ; *Plagiopholis* Blgr., mountains of Burma ; *Polyodontophis* Blgr., Mad., Comoros, S.-E. As., C. Am. ; *Prymnomiodon* Cope, Siam ; *Pseudoxenodon* Blgr., E. Indies, S. China ; *Pseudoxyrhopus* Gthr., Mad. ; *Rhabdops* Blgr., India, S. China ; *Simocephalus* Gthr., trop. and S. Afr. ; *Sureptophorus* D. and B., C. Am., N.-W. S. Am. ; *Tetralepis* Boet., Java ; *Trachischium* Gthr., E. Himalayas, Khasi Hills ; *Tretanorhinus* D. and B., C. Am., Cuba ; *Trirhinopholis* Blgr., Burma ; *Tropidonotus* Kuhl, Eur., As., Af., N. Aust., N. and C. Am., 74 species ; *T. natrix*, grass-snake, of this country, is widely distributed, but absent from Scotland and Ireland, can climb trees and swim, oviparous ; pair in May, June ; lay in July, August in rich vegetable soil ; to 6 ft., average 3 ft. ; *Xenochrophis* Gthr., S.E. As. ; *Xylophis* Beddome, S. India.

II. Genera in which the hypapophyses are absent on the posterior dorsal vertebrae, arranged alphabetically.

*Abastor* Gr., N. Am. ; *Ablabes* D. and B., S.-E. Asia, Japan ; *Aporophis* Cope, S. Amer. ; *Arrhyton* Gthr., Cuba ; *Atractus* Wagl., C. and S. Am., about 25 species ; *Calamaria* Boie, from Assam, Burmah and S. China to Malay Arch., about 35 species ; *Carphophis* Gerv., N. Am. ; *Cemophora* Cope, N. Am. ; *Chilomeniscus* Cope, Lower California ; *Chlorophis* Hallow, trop. and S. Afr. ; *Coluber* L., Eur., As., N. and trop. Amer., about 50 species. *C. quatuorlineatus* Lacép. to 6 ft., Italy, S.E. Eur., S. Tyrol ; *C. leopardinus* Bp., S. Italy, S.E. Eur., As. Min. ; *C. longissimus* Laur., aesculap Snake. S. France, Italy, S.E. Eur. ; *Contia* B. and G., S.-W. Asia and Sind, Am., about 20 species ; *Coronella* Laur., Eur., S.-W. As., India, N. Amer., about 20 species ; *C. laevis* Lac. (*austriaca*), the smooth snake, found in England, superficially resembles the viper but with round pupils, to 2 ft. ; *Cyclagras* Cope, S. Am. ; *Dendrelaphis* Blgr., India, Ceylon, Burma, Malay Pen. and Arch. ; *Dendrophis* Wagl., S.-E. As., Aust., tree-snakes ; *Dimades* Gr., S. Am. ; *Dinodon* D. and B., China, Japan ; *Dirosema* Blgr., C. Am. ; *Drepanodon* Per., S. Am. ; *Dromicus* Bibr., W. Indies, Chili, Peru ; *Drymobius* Cope, Am., Texas to Peru ; *Dryocalamus* Gthr., S.-E. As. ; *Farancia* Gr., N. Am. ; *Ficimia* Gr., Arizona, Texas, Mexico ; *Gastropyxis* Cope, W. Afr. ; *Geagras* Cope, Mexico ; *Geophis* Wagl., C. and S. Am. ; *Gonyophis* Blgr., Malay Pen., Borneo ; *Grayia* Gthr., trop. Afr. ; *Hapsidophrys* Fisch., W. Afr. ; *Herpetodryas* Wagl. ; *Heterodon* Latr., N. Am. ; *Homalosoma* Wagl., Afr. ; *Hydromorphus* Ptrs., C. Am. ; *Hydrops* Wagl., S. Am. ; *Hypsiglena* Cope, S. N.-Am., C. Am., Venezuela ; *Hypsirhynchus* Gthr., S. Domingo ; *Idiopholis* Mocq., Borneo ; *Leptocalamus* Gthr., trop. Amer. ; *Leptophis* Bell, C. and S. Am., tree snakes ; *Liophis* Wagl., Am., W. Indies, about 20 species ;



*Lycodon* Boie, S. As.; *Lystrophis* Cope, S. S.-Am.; *Lytorhynchus* Ptrs., N. Afr., As., Arizona, California; *Macrocalamus* Gthr. *Oligodon* Boie, S. As., Lower Egypt, about 20 species; *Petalognathus* D. and B. trop. Am.; *Philothamnus* Smith, trop. and S. Afr.; *Phrynonax* Cope, trop. Am.; *Prosymna* Gr. trop. and S. Afr.; *Pseudaspis* Cope, S. Afr.; *Pseudorhabdium* Jan, Malay Pen. and Arch.; *Rhabdophidium* Blgr., Celebes; *Rhadinaea* Cope, C. and S. Am., 26 species; *Rhamnophis* Gthr., trop. Afr.; *Rhinochilus* B. and G., N. Am., Mexico, Venezuela; *Scaphiophis* Ptrs., trop. Afr.; *Simophis* Ptrs., Brazil; *Simotes* D. and B., S. China, E. Indian continent and Arch., about 25 species; *Spilotes* Wagl., S. Am.; *Stegonotus* D. and B., Philippines, Moluccas, Papuasias, Queensland; *Stilosoma* Brown, Florida; *Symphimus* Cope, Mexico; *Sympholis* Cope, Mexico; *Synchalinus* Cope, C. Am.; *Thrasops* Hallow, W. Afr.; *Trimetopon* Cope, C. Am.; *Tropidodipsas* Gthr., C. Am.; *Typhlogophis* Gthr., Philippines; *Uromacer* D. and B., Santo Domingo; *Urotheca* Bibr., Cuba, C. and S. Am.; *Virginia* D. and B., N. Am.; *Xenelaphis* Gthr., Burma, Malay Pen. and Arch.; *Xenodon* Boie, trop. Am.; *Xenurophis* Gthr., W. Afr.; *Zamenis* Wagl., Eur., As., N. Afr., Senegambia, N. and C. Am., 31 species; *Z. mucosus*, rat-snake of India, to 7 ft.; *Z. constrictor*, the black-snake of America, to 6 ft. an expert climber; *Zaocys* Cope, S.-E. As. The position of *Amastridium* Cope, Colombia, and *Anoplophallus* Cope, Tahiti is doubtful.

Sub-fam. 3. **Rhachiodontinae.** Only a few teeth on the posterior part of the maxillary and dentary bones and on the palatines. Some of the anterior thoracic vertebrae with the hypapophysis much developed, directed forwards and capped with enamel; one genus and species. *Dasypeltis scabra* L., to 2½ ft., trop. and S. Afr.; they eat birds' eggs which they break in transit along the oesophagus with the hypapophyses above mentioned.

#### Series B. OPISTHOGLYPHA.

One or more of the posterior maxillary teeth grooved in front; more or less poisonous but not seriously harmful to man, the poison being weak or the poison teeth too far back; about 300 species, cosmopolitan except New Zealand, terrestrial, arboreal, and aquatic.

Sub-fam. 4. **Homalopsinae.** Nostrils valvular on the upper surface of the snout; viviparous, aquatic in the rivers and estuaries of the E. Indies from Bengal to N. Australia. *Hypsirhina* Wagl.; *Homalopsis* Kuhl; *Cerberus* Cuv.; *Eurostus* D. and B.; *Myron* Gr.; *Gerardia* Gr.; *Fordonia* Gr.; *Cantoria* Gir.; *Hipistes* Gr.; *Herpeton* Wagl.

Sub-fam. 5. **Dipsadomorphinae.** Nostrils lateral, dentition well developed; long-tailed, terrestrial, arboreal, and subaquatic; about 70 genera, cosmopolitan except the northern parts of the N. Hemisphere.

*Amblyodipsas* Ptrs., Mozambique; *Alluandina*, Mocq., Mad.; *Amplorhinus* Smith, trop. and S. Afr.; *Aparallactus* Smith, trop. and S. Afr.; *Apostolepis* Cope, S. Am.; *Brachyophis* Mocq., Somaliland; *Calamelaps* Gthr., trop. Afr.; *Chamaetortus* Gthr., E. and C. Afr.; *Chrysopelea* Boie, S.-E. As.; *Coelopeltis* Wagl., S. Eur., S.-V.



As., N. Afr.; *Conophis* Ptrs., Mexico, C. Am., S. Brazil; *Dipsadoboa* Gthr., W. Afr.; *Dipsadomorphus* Fitz., trop. Afr., S. As., Papuasias, Aust., about 22 species; *Ditypophis* Gthr., Socotra; *Dispholidus* Duv., trop. and S. Afr.; *Dromophis* Ptrs., trop. Afr.; *Dryophiops* Jan, S.-E. As.; *Dryophis* Dalman, S.-E. As.; *Elapomoius* Jan, Brazil; *Elapomorphus* Wieg., S. Am.; *Elapops*, Gthr., W. Afr.; *Elapotinus* Jan; *Erythrolamprus* Wagl., trop. Am., Texas; *Eteirodipsas* Jan, Mad.; *Geodipsas* Blgr., Mad.; *Hemirhagerrhis* Boettg., E. Afr.; *Himantodes* Cope, Mexico to trop. S. Am.; *Hologerrhum* Gthr., Philippines; *Homalocranium* D. and B., trop. Amer., about 25 species; *Hydrocalamus* Cope, C. Am.; *Ialtris* Cope, S. Domingo; *Ithyocyphus* Gthr., Mad., Comoros; *Langaha* Brug., Mad.; *Leptodira* Gthr., trop. and S.-Afr., trop. Am. to Texas; *Lycodryas* Gthr., Comoros; *Lycognathus* D. and B., trop. S.-Am.; *Macrelaps*, Blgr., S. Afr.; *Macroprotodon* Guichen., Spain and N. Afr.; *Manolepis* Cope, Mexico; *Microlaps* Boettg., Palestine, Somaliland; *Mimophis* Gthr., Mad.; *Miodon* Dum., W. Afr.; *Ogmilus* Cope, Mexico; *Oxybelis* Wagl., trop. Am.; *Oxyrhopus* Wagl., C. and S. Am., about 20 species; *Philodryas* Wagl., S. Am., about 13 species; *Polemon* Jan, W. Afr.; *Psammodynastes* Gthr., S.-E. As.; *Psammophis* Wagl., Afr. and S. As., 17 species; *Pseudablubes* Blgr., S. Brazil, Uruguay; *Pythondipsas* Gthr., trop. Afr.; *Rhamphiophis* Ptrs., trop. Afr.; *Rhinobothryum* Wagl., trop. S. Am.; *Rhinocalamus* Gthr., E. Afr.; *Rhinostoma* Fitz., S. Am.; *Scolecophis* Cope, C. Am.; *Stenophis* Blgr., Mad., Comoros; *Stenorhina* D. and B., Mexico, C. Amer., Colombia, Ecuador; *Tachymenis* Wieg., Bolivia, Peru, Chili; *Taphrometopon* Brandt, C. As., and Persia; *Tarbophis* Fleischm., S.-E. Eur., S.-W. As., trop. and N. E. Afr.; *Thamnodynastes* Wagl., S. Am.; *Thelotornis* Smith, trop. and S. Afr.; *Tomodon* D. and B., S. Am.; *Trimororhinus*, Afr. S. of Eq., E. Afr.; *Trimorphodon* Cope, California to C. Am.; *Trypanurgos* Fitz., trop. S. Am.; *Xenocalamus* Gthr., trop. Afr.; *Xenopholis* Ptrs., S. Am.

Sub-fam. 6. **Elachistodontinae**. Only a few teeth on the posterior part of the maxillary and dentary bones and on the palatines and pterygoids; some of the anterior thoracic vertebrae with the hypapophysis much developed and capped with enamel one genus and species. *Elachistodon westermanni* Reinh., Bengal.

#### Series C. PROTEROGLYPHA.

Anterior maxillary teeth grooved or perforated; behind these poison fangs a series of smaller solid teeth; all extremely poisonous and most are viviparous.

Sub-fam. 7. **Hydrophinae**. Sea-snakes. Tail strongly compressed laterally, with the neural spines and hypapophyses very much developed. Body more or less compressed; eyes small with round pupil; marine (except one species of *Distira* confined to a fresh-water lake at Luzon in Philippines), entering tidal streams; except *Platurus* specimens of which have been found at some distance from water, exclusively aquatic; all are viviparous; as a rule they are not found in mid-ocean, and some of them at least visit the shores of low islands to give birth to their young; Indian and Pacific Oceans; about 10 genera and 50 species. *Hydrus* Schn., Indian and Pacific

Oceans; *Thalassophis* Schm., coast Java of; *Acalyptophis* Brgl., W.-trop. trop. Pacific; *Hydrelaps* Blgr., N. coast of Australia; *Hydrophis* Daud. (Fig. 200), Indian and Pacific Oceans, 22 species; *Distira* Lac., Indian and Pacific oceans, about 20 species; *Enhydris* Merr., coast of India to Chinese sea and New Guinea; *Enhydrina* Gr., Persian Gulf to New Guinea; *Aipysurus* Lac., Malay Arch., and W.-trop. Pacific; *Platurus* Daud., E. parts of the Indian and W. Pacific Oceans.

Sub-fam. 8. **Elapinae.** Tail cylindrical; hypapophyses more or less developed throughout the vertebral column; about 29 genera and 150 species; Africa, S. Asia, S. N.-America, Central and S. America, and Australia in which they constitute the bulk of the ophidian fauna; absent from Madagascar and New Zealand.



FIG. 200.—*Hydrophis bicolor* (Règne Animal).

*Acanthophis* Daud., Moluccas, Papuasia, Austr.; *A. antarcticus*, the death-adder of Australia; *Aspidelaps* Smith, S. Afr., Mozambique; *Boulengerina* Dollo, C. Afr.; *Brachyaspis* Blgr., Aust.; *Bungarus* Daud., S.-E. As.; *B. candidus* L., the krait, Indian sub-region; *Callophis* Ptrs., S.-E. As.; *Dendraspis* Schleg., trop. and S. Afr.; *Denisonia* Krefft, Aust., Tasmania, Solomons, 21 species; *Diemenia* Gthr., Aust., N. Guinea; *Dolicphis* Gir., Burma, Cochin China, Malay Pen. and Arch.; *Elapechis* Blgr., trop. and S. Afr.; *Elapognathus* Blgr., Aust.; *Elaps* Schn. (Fig. 201), America, about 30 species; *Furina* D. and B., Aust.; *Glyphodon* Gthr., N. Guinea and N. Aust.; *Hemibungarus* Ptrs., S.-E. As.; *Homorelaps* Jan, S. Afr.; *Hoplocephalus* Gthr., Aust.; *Micropechis* Blgr., N. Guinea, Solomons; *Naia* Laur., Afr., S.-Asia, the neck region can be expanded into a hood by the spreading and moving forwards of the

ribs; *N. tripudians*, Merr., cobra, from Transcaspia to China and the Malay Islands, to 6 ft.; *N. haje* L., the aspis or spy-slange of Africa; *N. bungarus* Schleg., the hamadryad, King-Cobra, Snake-eating Cobra, to 12 ft., India to S. China and the Philippines; *Notechis* Blgr., Aust., Tasmania; *N. scutatus*, tiger snake; *Ogmodon* Ptrs., Fiji; *Pseudechis* Wagl., Aust., N. Guinea; *Ps. porphyriacus*, the black-snake (females "brown-adders") of Australia; *Pseudelaps* D. and B., Aust., Moluccas, Papuasia; *Rhinhoplocephalus* F. Müll., Aust.; *Rhynchelaps* Jan, Aust.; *Sepedon* Merr., S. Afr.; *S. haemachates*, the ringhals, S. Afr.; *Tropidechis* Gthr., Aust.; *Walterinnesia* Lataste, Egypt.

Fam. 8. **Amblycephalidae.** Facial bones slightly moveable, prefrontals not in contact with nasals, ectopterygoid present, these characters, as in *Colubridae*; differ from *Colubridae* in fact that pterygoids do not reach quadrate; externally distinguishable from *Colubridae* by absence of longitudinal median mental groove; they resemble in their head and neck poisonous snakes, but are harmless; S.-E. Asia, C. and S. America. *Haplopetura* Blgr., Pinang, Malay Arch.; *Amblycephalus* Kuhl., S.-E. As. *Leptognathus* D. and B., C. and S. Am.; *Dipsas* Laur., S. Am.; *Pseudopareas* Blgr., S. Am.

Fam. 9. **Viperidae.** Facial bones moveable, prefrontal not in contact with nasal, ectopterygoid present; squamosal present, loosely attached and suspending quadrate; maxillary short, erectile perpendicularly to ectopterygoid and carrying a pair of large perforated fangs without external groove, without other teeth; teeth on palatine and pterygoid; mandible without coronoid bone; hypapophyses throughout vertebral column; poisonous; all excepting *Atractaspis* viviparous; includes terrestrial, semiaquatic, arboreal, and burrowing types; Europe, Asia, Africa (absent from Madagascar), America.

Sub-fam. 1. **Viperinae.**

Without sensory pit on the side of the snout, maxillary not hollowed out above; Old World, except Madagascar. *Causus* Wagl., trop. and S. Afr.; *Azemiops* Blgr., Upper Burma; *Vipera* Laur., Eur., Asia, N. and trop. Afr.; *V. berus* L., the common European viper, to 28 inches, bite as a rule not fatal, *V.*

*russellii* Shaw, the daboia, to 5 ft., India, Ceylon, Burma, Siam *Bûis* Gr., Africa, *B. arietans* Wagl., puff-adder, to 5 ft., very poisonous, Afr., S. Arabia. *Pseudocerastes* Blgr., Persia; *Cerastes* Wagl., N. Afr., Arabia, Palestine, *C. cornutus* L., horned viper; *Echis* Merr., Afr. n. of equator, S. Asia. *Atheris* Cope, trop. Afr.; *Atractaspis* Smith, trop. and S. Afr.

Sub-fam. 2. **Crotalinae.** Pit-vipers. With a deep pit on each side of the snout between the nostril and the eye; maxillary hollowed out above; America, S. Asia; includes rattle-snakes which are confined to America. Without rattle are, *Ancistrodon* Baird, Caspian, As., N. and C. Am., about 10 species; *A. piscivorus* Lac., water-viper, E. N.-Am.; *A. contortrix* L., the copper-head, N. Am. *Lachesis* Daud., S.-E. As., N. and S. Am., about 40 species. With rattle are,



FIG. 201.—*Elaps corallinus* (Règne Animal).

*Sistrurus* Garm., N. Am. E. of Rockies, Mexico; and *Crotalus* L., Am. (not in the W. Indies), about 11 species; *C. horridus* L., common rattle-snake of U.S.; *C. durissus* L., to 8 ft., S.-E. U.S.; *C. terrificus* Laur., S. Amer.

### Sub-class 3. CROCODILIA.\*

*Lizard-like long-tailed Reptiles, usually of considerable or moderate size, with immoveable quadrates, a hard palate, and a quadrato-jugal arch, and with teeth implanted in alveoli of the jaws to which they are confined; with loose abdominal ribs, sternum and interclavicle, a sacrum composed of two vertebrae. The ventricle is divided by a complete septum. Anal opening longitudinal.*

Crocodiles are scaly animals, the scales consisting of cornifications of the epidermis. They have two pairs of limbs of which the anterior have five digits, the posterior four. The three preaxial digits in each limb possess nails. The hind feet are more or less webbed. The nostrils are placed at the end of the long snout and can be closed. The tympanic membranes are exposed, but can be covered over by a cutaneous fold. The eyes have vertical pupils, two lids and a nictitating membrane. There is a bony plate in the upper eyelid. They all possess on the back, and sometimes (*Caiman*, *Teleosaurus*, *Stagonolepis*) on the belly, a dermal skeleton of bony plates, which are arranged in transverse rows and correspond in form to the overlying epidermal scales. The bony plates of the back are pitted and sculptured and frequently keeled; the ventral plates are less sculptured, not keeled, and are sometimes composed of two sutured pieces, a small anterior and a large posterior. On the tail these plates form a dentated dorsal crest, paired in front, but single behind.

The vertebral column is marked out into cervical, dorsal,

\* Cuvier, "Sur les différentes espèces de Crocodiles vivants et leur caractères distinctifs." *Ann. du Mus. d'hist. Nat.*, 10, 1807. R. Owen, "Palaeontology," London 1860. Huxley, "On the dermal armour of Jacare and Caiman, etc." *Journ. Proc. Lin. Soc.*, 4, 1860. Rathke, "Untersuch. üb. d. Entwick. u. d. Körperbau der Crocodile," Braunschweig, 1866. Huxley, "On *Stagonolepis robertsoni* and on the evolution of the Crocodilia," *Quart. J. Geol. Soc.* 31, 1875, p. 423. Id., "Crocodilian remains in the Elgin Sandstone," *Memoirs of the Geological Survey of the United Kingdom*, monograph iii., 1877. Cope, "Crocodilians, Lizards and Snakes of N. America," *Rep. U. S. Nat. Mus.*, 1898. Boulenger, "Catalogue of Chelonians and Crocodiles in the British Museum," 1889. Hoffman, Gadow, Zittel, *op. cit.*



lumbar, sacral, and caudal regions (Fig. 202). There are 24 or 25 presacral vertebrae, 35 or more caudal and two sacral. The presacral vertebrae are usually distributed as follows: nine cervical, eleven or twelve dorsal, and three or four lumbar. In living crocodiles and in extinct species from the Cretaceous onwards, all the vertebrae except the atlas and axis (epistropheus), the second sacral, and the first caudal, are procoelous. The second sacral is flat in front and concave behind, and the first caudal is biconvex. In precretaceous forms the centra are feebly amphicoelous. The centra are united by discs of fibro-cartilage and the neurocentral suture persists.

All the cervical vertebrae have ribs. The atlas consists of four pieces, an unpaired ventral, two lateral, and a dorsal. The ventral piece carries a pair of backwardly projecting single-headed ribs; the dorsal piece is developed in membrane and has been interpreted as the remnant of the neural arch of a vanished *proatlas* vertebra. The axis has an odontoid process, which is suturally joined to it. A two-headed rib is attached to the odontoid process. The other cervical vertebrae all possess two-headed overlapping ribs, of which the capitulum articulates with a facet or small tubercle on the centrum, and the tuberculum with a short transverse process projecting from the neural arch above the neuro-central suture. In the first and second dorsal vertebrae the capitular tubercle is on the neurocentral suture, and in the third dorsal it has risen above this and is on the transverse process. In the succeeding vertebrae the point of attachment of the capitulum gradually moves outwards until it becomes joined to the tubercular attachment, and there is only one attachment for the rib, at the end of the transverse process. The lumbar vertebrae are without ribs and have long transverse

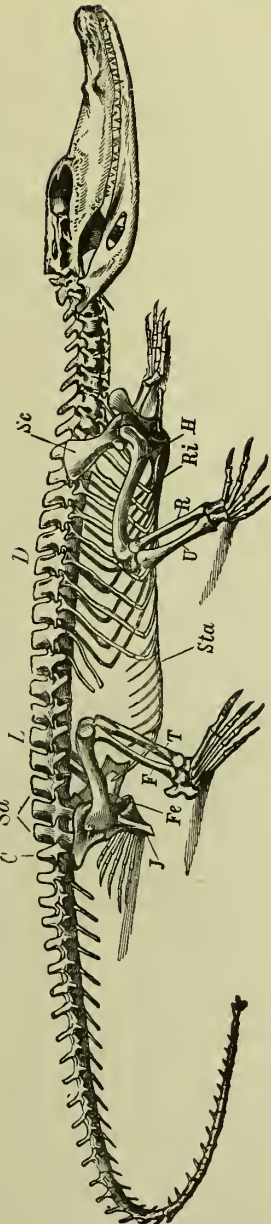


FIG. 202.—Skeleton of Crocodile. *C* first caudal; vertebra; *D* dorsal (thoracic) region; *F* fibula; *Fe* femur; *H* humerus; *J* ischium; *L* lumbar region; *R* radius; *Ri* ribs; *Sa* sacral region; *Sc* scapula; *Sta* abdominal ribs; *T* tibia; *U* ulna.



processes arising from the neural arch. In the sacral vertebrae the ribs are attached to the centrum and neural arch. The anterior caudal vertebrae bear ribs ankylosed to the centrum and neural arch. Chevron bones are present, attached to the posterior part of the centra of the caudal vertebrae, except on the first and the posterior vertebrae.

The **sternum** consists anteriorly of a rhomboidal plate of cartilage to the sides of which are articulated the sternal portions of two thoracic ribs, and of a narrower posterior portion, also cartilaginous, which soon bifurcates and has attached to it from five to seven pairs of sternal ribs. A slender interclavicle lies on the ventral surface of the rhomboidal part of the sternum.

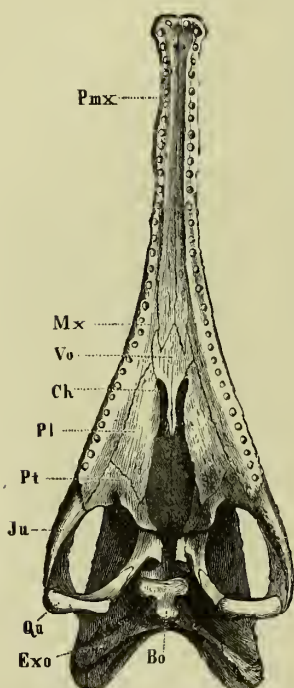


FIG. 203.—Ventral view of skull of *Belodon kapfi* to show the parasuchal choanae (after Zittel). *Bo* basioccipital; *Ch* choanae; *Exo* exoccipital; *Ju* jugal; *Mx* maxilla; *Pl* palatine; *Pmx* premaxilla; *Pt* pterygoid; *Qu* quadrate; *Vo* vomers.

The **thoracic ribs** (Fig. 202) consist of a vertebral portion of which the distal part is feebly ossified, and of a sternal portion also feebly ossified and joining the sternum. The former in the case of several of the anterior ribs carry on the hinder side of their dorsal more ossified portion an *uncinate* process in the form of a small cartilaginous (sometimes partly ossified) plate.

The so-called "*abdominal ribs*" (Fig. 202, *Sta*) are membrane bones placed on the ventral surface of the rectus abdominis muscles. They are usually seven in number and consist on each side of

two curved rods; they are not joined in the middle line.

In the skull the dorsal and lateral bones are roughly pitted. There is a low cartilaginous interorbital septum with a membranous interspace, and the presphenoid and orbitosphenoid region remains cartilaginous. There is an alisphenoid, and a separate prootic, but the epiotic fuses with the supraoccipital and the opisthotic with the exoccipital. The occipital condyle

is formed by the basi-occipital only, and the exoccipitals meet above the foramen magnum. The parietals and frontals are unpaired in the adult. The nostrils are single, placed at the front end of the skull and entirely surrounded by the premaxillaries. The nasals are long, but do not reach the anterior nares. They usually reach the premaxillaries, but in *Gavialis* are separated from them by the maxillaries. The vomers are double and by their opposed vertical plates separate the narial passages. The premaxillae, maxillae, and palatines develop palatal plates which unite in the middle line and form a hard palate, and in all living crocodiles and in extinct crocodiles from the Cretaceous onwards, the pterygoids are modified in the same way, so that the internal narial opening is placed far back on the base of the skull (*Eusuchia* of Huxley, Fig. 205). In precretaceous crocodiles the pterygoids do not develop palatal plates and the posterior nares are behind the palatines (*Mesosuchia* of Huxley, Fig. 204). An ectopterygoid or transpalatine connects the pterygoid with the maxilla and jugal (Fig. 204, *T*).

Prefrontals, lacrymals (unperforated), and postfrontals are present. The orbit is separated from the temporal fossa by the post-orbital bar formed by processes of the post-frontal and jugal. Both supra-temporal and infra-temporal arcades are present, the former constituted by the postfrontals and squamosals, the latter by the jugal and quadrato-jugal. The quadrate is large, projects backwards and is overlaid by the squamosal; it is immoveably fixed to the skull.

The tympanic cavity is well surrounded by bone. It communicates with the pharynx by a complicated system of eustachian canals, and gives off air-passages into the surrounding bones. Of these, the air-passages of the quadrate communicate by a membranous tube (*siphonium*) with an air space in the os articulare of the mandible, and a passage running through the bones of the posterior part of the roof of the skull puts the two tympanic cavities in communication.

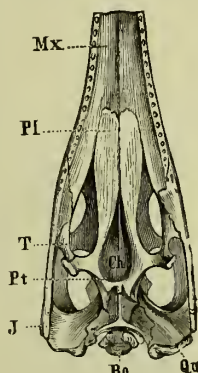


FIG. 204. — Ventral view of skull of *Pelagosaurus temporalis* Blv., to show the mesosuchal choanae (after Zittel). *Bo* basioccipital; *Ch* choanae; *J* jugal; *Mx* maxilla; *Pl* palatine; *Pt* pterygoid; *Qu* quadrate; *T* transpalatine (ectopterygoid).

The eustachian passages \* are surrounded by bone and open close together into the pharynx by a median opening behind the posterior nares. From this opening (Fig. 206) there passes off three tubes, one median and two lateral. The median tube (*o*) is contained in a canal between the basioccipital and basisphenoid, where it bifurcates into an anterior branch (*q*) which passes into the basisphenoid, and a posterior into the basioccipital (*r*). The anterior branch divides into a right and left canal which open into the tympanic cavity. The posterior also bifurcates and each of

the canals so formed (*s*) runs to open into the tympanic cavity by a tube (*t*), which joins one of the two lateral canals (*p*) which pass from the pharyngeal opening.

The columella is bony and extends from the fenestra ovalis to articulate with a trifold cartilage—the extra-columellar cartilage (infra- + extra- + supra-stapedial), which is attached to the tympanic membrane.

The lower process of this cartilage is continuous with a partly cartilaginous, partly fibrous cord which lies in a groove or canal on the hinder surface of the quadrate immediately behind the siphonium, and is connected with the os articulare of the lower jaw. The upper cartilaginous part of this cord is called by Huxley the styloid cartilage. In the embryo this cord was a continuous cartilaginous connection between the lower process (infra-stapedial) of the extra-columellar cartilage and Meckel's cartilage.

The hyoid consists of a cartilaginous body and a pair of partly ossified cornua.

The lower jaw consists of six bones, the *dentary* which suturally unites with its fellow at the symphysis and bears the sockets in which the teeth are implanted; the *splénial* (*operculare*), the *angular*, the *surangular*, the *articular* which is pneumatic, and the *coronoid*. In the long-snouted forms the splénial may take part in the symphysis.

Owen, *Phil. Trans.*, 1850; v. Beneden, *Arch. de Biologie*, 3, 1882, p. 497.

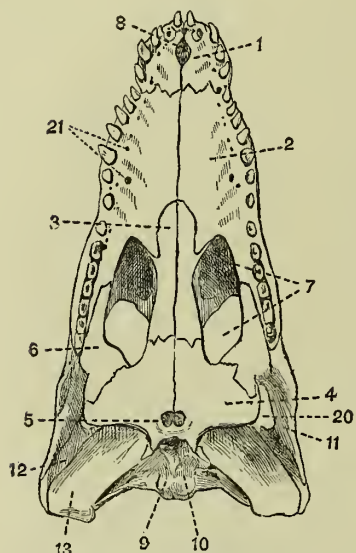


FIG 205.—Ventral view of skull of an alligator (*Caiman latirostris*) to show eusuchal choanae (after Reynolds). 1 premaxilla; 2 maxilla; 3 palatine; 4 pterygoid; 5 choanae; 6 transpalatine; 7 posterior, 8 anterior palatine vacuity; 9 basioccipital; 10 median opening of the eustachian tube; 11 jugal; 12 quadrato-jugal; 13 quadrate; 20 lateral temporal fossa; 21 vascular channels leading into openings of alveolar sinus.

The pectoral girdle consists of a scapula with a dorsal cartilaginous suprascapula margin, and of a coracoid without a fenestra. The coracoid articulates with the sternum. There is no clavicle, but an interclavicle lies on the sternum. There are five digits in the manus.

The carpus consists of six pieces : a radiale, an ulnare which articulates with the pisiform and radiale, but does not reach the ulna, and a pisiform in the proximal row ; in the distal row there is a piece of cartilage representing carpal 1 and 2, and a bone (*lenticular*) representing carpal 3, 4, and 5. In addition there is a small cartilaginous centrale on the distal surface of the radiale. The three radial digits are stronger than the two ulnar and bear claws.

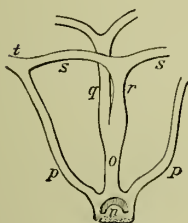


FIG. 206.—Diagram of the passages connecting the tympanic cavities with the pharynx in *Crocodilus* (after Owen, from Gegenbaur). *n* valve at the pharyngeal opening; *o* median canal, which divides into an anterior *q* and a posterior *r*; for *s*, *t*, *p* see text.

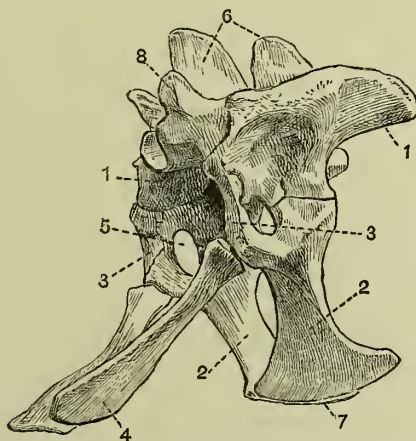


FIG. 207.—Pelvis and sacrum of an alligator (*Caiman latirostris*)  $\times \frac{1}{2}$  (after Reynolds). 1 ilium; 2 ischium; 3 forward process of ischium; 4 pubis; 5 acetabular foramen; 6 neural spines of sacral vertebrae; 7 symphysis ischii; 8 prezygapophysis.

In the pelvis (Fig. 207) the ilia are attached to the two sacral ribs ; the ischium is large and is joined to its fellow in a ventral symphysis by synchondrosis. The pubis is directed forwards and is excluded from the acetabulum by a forward process of the ischium. The ventral end of the pubis remains cartilaginous, and extends forwards as an epipubis. In front the two epipubes are separate, but behind they are united by a broad and strong ligamentous band. There are four digits in the pes, No. 5 being absent.

It is sometimes stated that there is no pubic or ischiadic symphysis. But though it is true that the bones do not meet and appear separate in



dry specimens, it must not be forgotten that they are close together and connected by strong cartilaginous or ligamentous bands.\*

The acetabulum is perforated. It has been contended that the pubis is represented by a small patch of cartilage between the anterior end of the ilium and the ischium, and that the pubis should be called an epipubis. It is doubtful if this contention can be maintained (*v. Huxley op. cit.*). The tarsus consists of two large proximal bones, an astragalo-navicular and a calcaneum, of which the calcaneum has a strong heel-process (Fig. 202); and of two small distal bones. The fifth digit is represented by an imperfect metatarsal attached to the fused tarsalia 4 and 5. The three pre-axial digits are clawed.

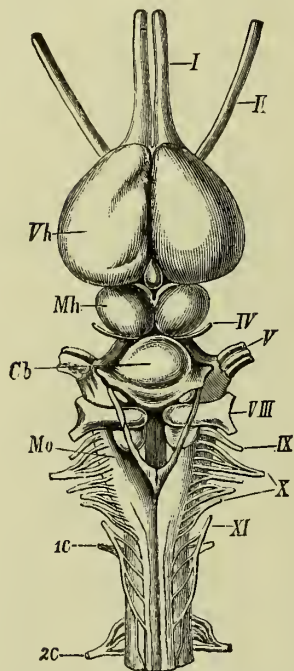


FIG. 208.—Brain of Alligator, dorsal view (after Rabl Rückhard, from Claus). *Cb* cerebellum; *Mh* optic lobes; *Mo* medulla oblongata; *Vh* cerebrum; roman numerals are cranial nerves; *1C*, *2C* first two spinal nerves.

The skin is horny on the scales but soft between. Each scale possesses a small pit in which the epidermis is not cornified; at the bottom of these pits are a number of tactile bodies in the cutis.

There are two pairs of musk secreting glands, one pair which can be everted on the throat, and another pair within the lips of the cloaca.

In the brain † the cerebellum is rather more developed than in other reptiles and possesses a median vermis and two small lateral lobes (Fig. 208). The eye ‡ is provided with a small (abortive) pecten. Lacrymal and harderian glands are present.

**Alimentary canal.** The teeth are in a single row on the premaxillae, maxillae and dentaries. They are lodged in sockets (thecodont) and are hollow, conical structures with-

out roots. They are shed at intervals and replaced by new teeth formed behind them and projecting as they grow into the pulp cavities of their predecessors. The fourth mandibular tooth is

\* Huxley, *Proc. Roy. Soc.*, 28, 1879, p. 395.

† Rabl-Rückhard, *Z. f. w. Z.*, 30, 1878, p. 337.

‡ D. W. Soemmerring, *De oculorum section-horizontal*, Göttingen, 1818, p. 59.



generally larger than the others. The tongue is flat and not protrusible. Salivary glands are absent. There is a transverse fold of the mucous membrane of the palate just in front of the choanae, which can shut off the mouth from the pharynx. The stomach is a gizzard-like sac, with muscular walls and tendinous discs. The pylorus is near the oesophageal opening. There is a gall bladder, but no caecum.

The cloaca is divided into two parts by a muscular fold. Into the anterior chamber open the urinary and generative ducts by separate and paired openings. There is no bladder. On the ventral side of the posterior chamber of the cloaca is a grooved penis \* very similar to that of the *Chelonia* (p. 410). Peritoneal canals are present in both sexes and open on either side into the cloaca at the base of this organ.

The testes are oval, the kidneys lobed, and the ovaries elongated.

The **trachea** is long and provided with complete rings. There is a larynx with vocal chords. The epiglottis is absent, and the larynx has an annular cartilage corresponding to the cricoid and thyroid of higher forms, and arytenoid cartilages. The lungs hang freely in the body cavity and are well developed and spongy. The bronchus enters at about the middle of the organ and is continued to its hind end; it soon loses its rings, and is beset with openings which lead into pouches, the walls of which are honeycombed.

The lungs lie in the anterior horns of the body-cavity. These are partitioned off from the rest by a septum † which is partly muscular and partly membranous and has peculiar relations to the liver and stomach. It is analogous but not homologous to the mammalian diaphragm and is said to assist in the inspiratory movements.

**Vascular system.** The sinus venosus is closely applied to the heart and receives the three great systemic veins. The ventricle is double. The right aortic arch proceeds from the left ventricle and gives off the arteries to the head and anterior limbs. These are an innominate and a right subclavian; the innominate divides into left subclavian and carotis primaria which divides into the two common carotids. The left aortic

\* Boas, Gadow *op. cit.*

† G. W. Butler, *P.Z.S.*, 1889, p. 452.

arch arises in the right ventricle and after giving off a large visceral artery is connected by a narrow vessel with the right arch (Fig. 209). The pulmonary artery also arises from the right ventricle. Each of these three great arteries is guarded at its ventricular end by two semi-lunar valves. At the point

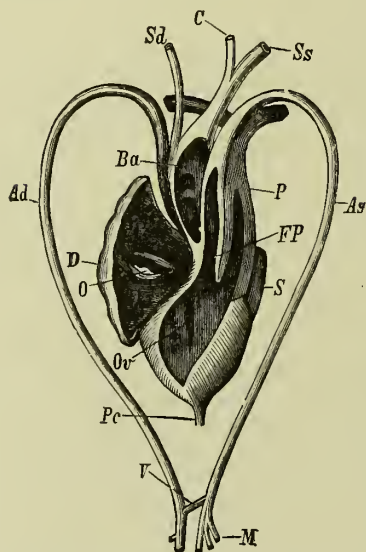


FIG. 209.—Heart and arterial arches of *Alligator lucius* (from Claus). The right auricle and right ventricle are opened and the arteries springing from the right ventricle. *Ad* right, *As* left aorta; *Ba* dilatation on right aorta; *C* carotis primaria; *D* right auricle; *FP* position of foramen Panizzæ; *M* visceral arteries; *O* opening of sinus venosus into right auricle; *Ov* opening of right auricle into right ventricle; *P* pulmonary artery; *Pe* band connecting to pericardial wall; *S* left auricle; *Sd* right, *Ss* left subclavian; *V* narrow continuation of left aortic arch after giving off the coeliac artery.

aperture (*foramen Panizzæ*) putting them in communication, so that the arterial and venous blood are not completely separated. The *Crocodylia* are the only Vertebrata with two separate ventricles, and both right and left aortic arches.

Crocodiles are fierce rapacious animals and live for the most part in fresh water; the gavials being more exclusively aquatic than the crocodiles and caimans. They inhabit the mouths and lagoons of great rivers in the warmer parts of the Old and New Worlds, and seek their prey by night. Some are dangerous to man. They all have a voice which is described as a "short bark." They appear to grow throughout life which is a long one. The eggs are hard-shelled and are laid in the sand or in holes on the banks.

The oldest *Crocodylia* which appear in the Upper Trias, belong to the *Parasuchia* and *Pseudosuchia*. Though undoubtedly *Crocodylia*, they present some features which are characteristic of the *Dinosauria* and *Rhynchocephalia*. The *Eusuchia* do not appear till the Upper Lias, and the earliest of these possess biconcave vertebrae, and choanae in front of the pterygoids. The earliest crocodiles appear to have been marine, and it is not

till after the Jurassic period that the majority are found in association with fresh-water and land forms. The living forms are inhabitants of fresh water, a few species extending into estuaries.

Huxley in his classical memoir on the "Crocodilia of the Elgin Sandstones" (*loc. cit.*) divided the Crocodilia into three groups which form a series in respect of certain osteological characters, viz. the structure of the palate, the condition of the eustachian passages, the form of the vertebrae, and one or two other points. These groups he named (1) the *Parasuchia* in which the palatines and pterygoids have no palatal plates (Fig. 203), the eustachian passages are unenclosed by bone and the vertebrae are amphicoelous; (2) the *Mesosuchia* with amphicoelous vertebrae, eustachian passages partly enclosed in bone, and palatal plates to the palatines but not to the pterygoids (Fig. 204); (3) the *Eusuchia* with procoelous vertebrae, eustachian passages completely embedded in bone, and palatal plates to both pterygoids and palatines (Fig. 205). He also showed that these groups succeed one another in time in a manner which is consistent with regarding them as having being derived successively from one another, i.e. the Mesosuchia from the Parasuchia, and the Eusuchia from the Mesosuchia. In short he showed that the Parasuchia appear in and are confined to the Trias, the Mesosuchia appear in the Upper Lias and are continued to the Wealden, while the Eusuchia extend from the Later Cretaceous to the present time. To use Huxley's words: "The order of occurrence of the three divisions of the *Crocodilia* in time coincides with the order in which they depart from the lacertilian type and put on special crocodilian characters; and this palaeontological fact is in precise accordance with the needs of the theory of evolution."

In the following systematic treatment of the group, this division of Huxley has been partly followed, but the Mesosuchia, which more closely resemble the Eusuchia than they do the Parasuchia, have been united with the Eusuchia, and a new group the Pseudosuchia has been established for certain imperfectly known forms discovered since the date of Huxley's memoir.

#### Order 1. PARASUCHIA.\*

Extinct *Crocodilia* of considerable size, confined to the Triassic formation (Keuper), Europe, Asia, and N. America. With two longitudinal rows of dorsal scutes, and more numerous rows of ventral scutes (composed of one piece only), biconcave vertebrae, long premaxillae, external nostrils placed far back near the upward directed orbits, internal nares at the front end of the palatines (Fig. 203). The palatines and pterygoids do not meet in the middle line, and the eustachian passages are not enclosed by bone. A postorbital behind the orbit. Parietals and frontals paired. Acetabulum formed of ilium, ischium and pubis. A clavicle is present. In the separate, posteriorly placed nostrils, in the large preorbital fossae, in the form of the pterygoids and basiphenoid they resemble the Dinosaurs. In some other characters (e.g. the separate postorbitals, the paired parietals and frontals, the palate, the well developed ventral ribs, and the clavicle) they approach the *Rhynchocephalia*. *Belodon* v. Meyer, *Stagonolepis* Ag., *Parasuchus*, Huxl.

\* Huxley, *Quart. J. Geol. Soc.*, 1859, 15, p. 440, and 1875, 31, p. 423.

## Order 2. PSEUDOSUCHIA.\*

Extinct Triassic (Keuper) *Crocodylia* found in Germany, Scotland, and New Mexico. With short premaxillae, anterior and laterally-placed nostrils, large orbits, teeth in anterior part of jaw only, two rows of bony plates on the back. *Aëtosaurus* Fraas, *Ornithosuchus* Newton, and *Erpetosaurus* Newton from the Elgin Sandstone, *Typothorax* Cope, New Mexico.

## Order 3. EUSUCHIA.

(*Mesosuchia* and *Eusuchia* of Huxley, Crocodiles proper.)

With biconcave (in extinct forms) or procoelous vertebrae, short premaxillaries enclosing the nostril which is single and placed at the end of the snout; internal nares placed far back behind the palatines (Fig. 204), in recent forms in the hinder part of the pterygoids (Fig. 205). In the precretaceous forms and in some of the cretaceous, the median eustachian canal is enclosed in bone, but the lateral canals are represented only by grooves; parietals unpaired, clavicles absent, pubis not entering into the acetabulum. Anterior feet with five, posterior with four toes and traces of a fifth. When the snout is long, its elongation is due to the maxillaries. They are known since Lower Jurassic times. The living forms which with the exception of one species of *Alligator* found in China are intertropical, are grouped in two families and six genera.

Fam. 1. **Teleosauridae**. Snout long and slender, vertebrae biconcave, internal nares at the hinder end of the palatines, anterior limbs half the length of the posterior, nasals separated by a wide interval from the small premaxillaries, a small preorbital foramen, prefrontal small, lacrymal large. Two rows of large dorsal and several rows of smaller ventral bony plates. Lias and Oolite of Europe, marine. *Mystriosaurus* Kaup., *Pelagosaurus* Brown, *Stenosaurus* Geoffroy, *Teleosaurus* Geoff.

Fam. 2. **Metriorhynchidae**. Vertebrae biconcave, snout fairly long, nasals broad, internal nares at hind end of palatine, prefrontals large, lacrymal small, eyes within in sclerotic, skin without bony plates, Upper Jurassic, marine. *Metriorhynchus* v. Meyer, *Geosaurus* Cuv. etc.

Fam. 3. **Macrorhynchidae**. Vertebrae biconcave, snout long and slender, nasals narrow and long, internal nares at the hind end of the palatine, dermal armour of dorsal and ventral plates, in the fresh-water deposits of the Purbeck, Wealden and Greensand of Europe. *Macrorhynchus* Dunker, *Petrosuchus* Owen.

Fam. 4. **Atoposauridae**. Body small, lizard-like; snout short, rounded; vertebrae biconcave; without ventral dermal armour; Upper Oolite of France; marine. *Atoposaurus* v. Meyer, *Alligatorium* Jourdan, *Alligatorellus* Jourd.

Fam. 5. **Goniopholidae**. Vertebrae biconcave; snout moderately elongated; choanae far back between the palatines and pterygoids; with dorsal bony plates. Fossil in Purbeck, Wealden of Europe and Upper Jurassic of N. Amer. *Goniopholis* Owen, *Nannosuchus* Ow., *Theriosuchus* Ow., *Bernissartia* Dollo.

Fam. 6. **Gavialidae**. Vertebrae procoelous, teeth subequal, snout long and slender, nasals widely separate from nasal aperture, internal nares

\* Fraas, "Aëtosaurus ferratus," *Württemb. naturw. Jahreshfte*, 23, 1867. Newton E. T. *Phil. Trans.*, 185, 1894.



within the pterygoids; maxillae, palatines, and pterygoids with palatal plates. Littoral and marine deposits of the Upper Cretaceous of Europe and North America to present day. *Thoracosaurus* Leidy, Upper Cretaceous of N. Amer. and France; *Tomistoma* Müller,  $\frac{20-21}{18-19}$  teeth on each side; nasals in contact with premaxillaries, separate from nasal aperture; living in Borneo, fossil in Tertiaries of Europe. *Gavialis* Oppel,  $\frac{27-29}{25-26}$  teeth on each side; nasals separated from premaxillaries and from nasal aperture; without ventral bony scutes; living in India and Burma, fossil in the Pliocene of the Sivalik Hills; *G. gangeticus* Gray, N. India, Bombay, Aracan; harmless, and living on fish, to 20 feet. *Rhamphosuchus* from the Pliocene of the Sivalik Hills, to 50 feet.

Fam. 7. **Crocodylidae.** Vertebrae procoelous, nares anterior, nasals almost always reaching nasal aperture; choanae far back surrounded by the pterygoids; maxillaries, palatines, and pterygoids with palatal plates; orbit communicating with the infra-temporal fossa; ribs with uncinate processes; clavicles absent; pubis excluded from the acetabulum; 5 fingers, 4 toes; dorsal armour; pupil vertical. From the Upper Cretaceous to the present day, found in Europe until the Pleistocene. *Diplocynodon* Pomel, extinct, Oligocene and Miocene of Europe; *Bottosaurus* Ag., Upper Cretaceous of North America. *Crocodylus*, Laur., head long, teeth unequal, fourth mandibular tooth usually fitting into a notch in the upper jaws,  $\frac{16-19}{14-15}$  teeth on each side, without bony nasal septum, without ventral armour; Afr., S. Asia, N. Australia, trop. Amer., from the Upper Cretaceous to the Pleistocene in Eur. *Osteolaemus* Cope, fourth mandibular tooth as in the last, nasal bones dividing the nasal aperture, ventral scutes bony, W. Afr. one species. *Alligator* Cuv., head short and broad; teeth very unequal, fourth mandibular tooth fits into a pit of the upper jaw;  $\frac{17-20}{17-22}$  teeth on each side; nasal bones dividing nasal aperture; dorsal bony scutes not articulated together, ventral scutes without or with thin ossifications; two living species, one in China, and the other in N. Amer.; from fluviatile deposits of Upper Cretaceous to Pliocene in Eur. *Caiman* Spix (*Jacare* Gray), head, teeth, and fourth mandibular tooth, as in the last,  $\frac{17-20}{18-20}$  teeth on each side, without bony nasal septum, with dorsal and ventral armour of articulated bony scutes, 5 species, Central and South Amer.

#### Sub-class 4. DINOSAURIA.\*

*Long-tailed reptiles usually of considerable, often of gigantic size, with a superior and inferior temporal arcade, a fixed quadrate, and thecodont dentition; without pineal foramen. The limbs are adapted for the habitual support of the body, the ilium is extended antero-posteriorly, and the pelvis and hind limbs are generally bird-like in structure. The ribs are two-headed.*

The *Dinosauria* make their appearance in the Trias and persist until the Cretaceous. Their remains have been found in Europe, Asia, S. Africa, Madagascar, N. and S. America, and in Australia. It has been suggested that they were amphibious. This suggestion is based on the large size of

\* Also called the *Ornithoscelida*.



the tail which might conceivably have served as a swimming organ. However this may be the great number of them which have been found as fossils seems to indicate that they lived in swamps or in the neighbourhood of water, that is to say in places where their bodies would after death be rapidly covered by sediment. They have left their footprints in the sandstone (Triassic) of the Connecticut valley, and other parts of N. America. By their skull and one or two other features the Dinosauria present resemblances to Crocodilia and Rhynchocephalia, but in many of them the shoulder girdle, pelvis and hind limb are strongly avine in character.

#### Order 1. THEROPODA.

Digitigrade carnivorous Dinosaurs with cutting teeth, and small skull set at a right angle with the neck. The cranium is incompletely ossified

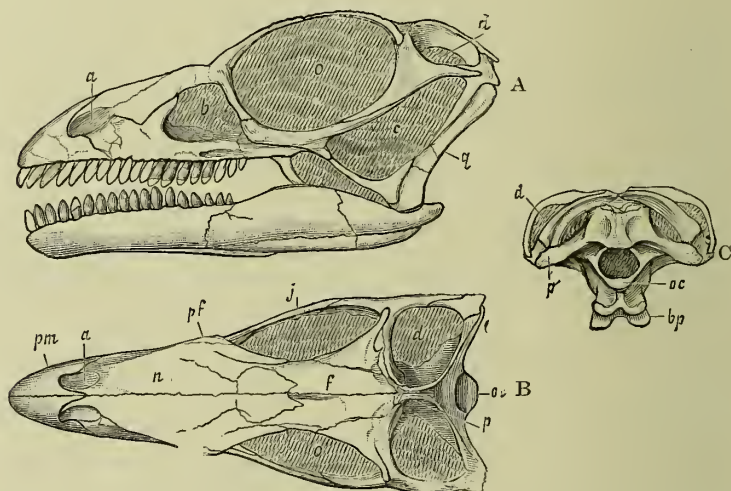


FIG. 210.—*Anchisaurus colurus*, skull, A from the side, B from above, C from behind (from Woodward, after Marsh).  $\times \frac{1}{2}$ . Trias, Connecticut. a external nostril; b preorbital vacuity; bp basiptyergoid vacuity; c lateral temporal fossa, d supratemporal fossa; f frontal; j jugal; n nasal; o orbit; oc occipital condyle; p parietal; p' paroccipital process; pf prefrontal pm premaxilla; q quadrate.

and there is a large preorbital vacuity (Fig. 210). The vertebrae are sometimes and the limb bones are always hollow. The fore-limbs are smaller than the hind-limbs and the progression was probably mainly bipedal. Both pubis and ischium meet in a ventral symphysis and there is no post-pubic process. The digits are from three to five and have prehensile claws. The astragalus sends up a process which is firmly fixed to the front side of the tibia. They vary much in size. *Compsognathus* the smallest Dinosaur was no larger than a cat, while *Megalosaurus* attained the dimensions of an elephant.

They extend from the Trias to the Cretaceous. They are the earliest Dinosaurs as yet known and are usually regarded as being the most generalised of the group.

*Anchisaurus* Marsh (Fig. 210), small forms with bird-like skull, Trias, Connecticut; and other allied genera from the U.S. *Zanclodon* Plien., Keuper, Württemberg, and several allied genera from France, England, India and S. Africa. *Ceratosaurus* Marsh, 17 feet, skull larger than usual, nasal bones with a median projection, which may have supported a horn, U. Jura, Colorado, and other genera. *Megalosaurus* Buckland, the largest Theropod, Lias to Wealden, Europe and N. America. *Allosaurus* Marsh. *Compsognathus* Wagner, vertebrae and limb bones hollow; the cervical vertebrae are elongated; the skull is bird-like; tail long; small anterior, long posterior limbs; manus and pes with 3 functional digits, digits 1 and 5 reduced; femur shorter than tibia; pelvis not avine, with pubic and ischiadic symphysis; pubis directed forwards; hind-limb very avine; astragalus with ascending process; one specimen only known, from the Solenhofen slates. *Hallopus* Marsh, very similar to preceding, manus with 4 digits, pes with 3, calcaneum with a heel process, astragalus without ascending process, U. Jura, Colorado. *Coelurus* Marsh, skull unknown, all bones hollow, U. Jura, England and N. America.

## Order 2. SAUROPODA.

Herbivorous, quadrupedal, plantigrade Dinosaurs with five hoofed

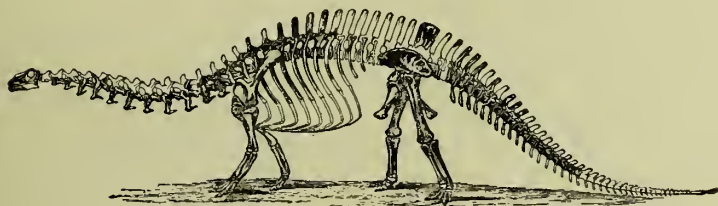


FIG. 211.—*Brontosaurus excelsus*  $\times \frac{1}{150}$  (from Woodward, after Marsh).

digits on each limb. The teeth are spatulate with anterior and posterior cutting edges. The cranium is completely ossified and there is a large preorbital vacuity. The anterior vertebrae are much hollowed out laterally. Limbs nearly equal in size. The neural canal in the sacrum is expanded to two or three times the size of the brain cavity. The bones of the pelvis are distinct and the acetabulum is perforated. The pubes project ventralwards and meet in a cartilaginous symphysis; there is no postpubis; the femur is without a prominent inner (fourth) trochanter; distal row of carpals and tarsals unossified; astragalus without ascending process. Some of them are of enormous size, and they are remarkable for the relatively minute size of the skull; *Atlantosaurus* estimated to have attained a length of 115 feet. The skull is in most of them imperfectly known. Their remains are known from the Jurassic and Cretaceous, *Cetiosaurus* Owen, skull unknown, M. Jura, England. *Atlantosaurus* Marsh, probably the largest land animal known, to 115 feet, U. Jura, Wyoming, Colorado. *Morosaurus* Marsh, U. Jura, Wyoming. *Brontosaurus* Marsh (Fig. 211), to 60 feet, very small skull and minute cranial cavity, U. Jura, Wyoming, Colorado. *Diplodocus* Marsh, teeth slender and cylindrical, continued to the anterior end of the jaws; the external narial opening is single and is placed at the apex of the skull, the nasals

being extremely shortened as in Cetaceans; cervical vertebrae elongated, 15 in number; 11 dorsals, 4 sacrals and 37 or more caudals; the neck and tail constitute the greater part of the animal, the head is very small; chevron bones double, each half with anterior and posterior prolongation; the curious position of the external nares may suggest aquatic habits, U. Jura, Wyoming and Colorado.

### Order 3. PRESENTATA.\*

Large herbivorous quadrupedal or bipedal Dinosaurs, with an edentulous prementary bone at the front end of the mandible, and a fully ossified brain case. The premaxillae are edentulous. The teeth are laterally compressed with serrated anterior and posterior cutting edges and are

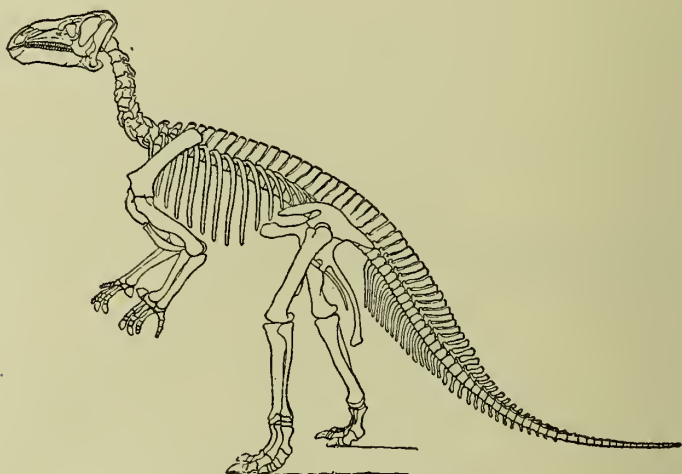


FIG. 212.—*Iguanodon bernissartensis*; restoration of skeleton by Marsh  $\times \frac{1}{80}$ . Wealden, Bernissart (from Woodward).

borne by the maxillae and dentaries. The pubis is slender, directed ventrally, but does not form a symphysis; there is a slender postpubis directed backwards parallel with the ischium which is also slender and meets its fellow in a ventral symphysis. The limb bones are solid or hollow. The manus has four or five digits, the pes three or four; the femur has a prominent distal inner (fourth) trochanter, and the astragalus is without an ascending process; dermal armour is present or absent. Jurassic and Cretaceous.

Tribe 1. **ORNITHOPODA**. Unarmoured, bipedal, digitigrade forms, with hollow limb bones. U. Jura and Cretaceous. *Iguanodon* Mantell (Fig. 212), so called from the resemblance of its teeth to those of *Iguana*, from the Wealden of England, Belgium and Germany, several complete skeletons of *I. bernissartensis* about 30 ft. in length have been discovered in the colliery of Bernissart in Belgium about 1,000 feet below the surface. The

\* Also called *Orthopoda*.

skull is laterally compressed, has a small orbit, and small preorbital vacuities; the premaxillae have a cutting edge and are edentulous; the maxillae and mandible bear the teeth which are often worn down to a grinding surface; the jugal is a crescentic bone below the orbit, and the quadrate is elongated. There are about 80 vertebrae (10 cervical, 18 dorso-lumbar, 4-6 sacral and 40-50 caudal); all bear ribs except the atlas, two or three lumbar, and the posterior caudal; the neural spines of the back and tail are very strong and frequently show traces of ossified tendons. The caudals have chevrons. The scapula is long, the coracoid small and there is a pair of sternal bones. Manus with 5 digits of which, the pollex is a spur-like process; digits 2 and 3 are tipped with hoof-like nails. The ilia are greatly extended antero-posteriorly: there is an ischiadic symphysis, and a slender postpubic process. The femur has a prominent inner (4th) trochanter and the pes has 3 digits with claw-shaped terminal phalanges. *Hypsilophodon* Huxley, complete skeleton from the

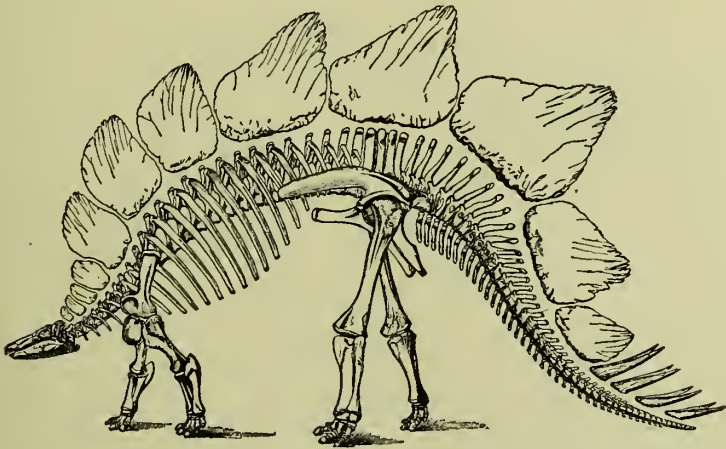


FIG. 213.—Skeleton of *Stegosaurus unguatus* (after Marsh, from Woodward); U. Jura, Colorado,  $\times \frac{1}{25}$ .

Isle of Wight. *Laosaurus* Marsh, U. Jura, Colorado; *Claosaurus* Marsh, U. Cretaceous, Wyoming; *Trachodon* Leidy, U. Cretaceous, U.S.A.

Tribe 2. **Stegosauria**. Armoured, quadrupedal plantigrade forms, with solid bones and small skull. Lias to U. Cretaceous. *Stegosaurus* Marsh (Fig. 213), head small; brain minute, smaller than the large sacral swelling of the spinal cord; teeth numerous and small; cervical vertebrae with ribs, neural spines expanded to support the dermal armour; sacrum of 4 fused vertebrae; anterior caudal vertebrae very large; fore-limb short, powerful, ulna with large olecranon process; ilium extends far forward; astragalus and calcaneum united with the tibia and fibula which are short; dermal armour of large triangular plates along the back and indications of small rounded ossicles on the throat, to 28 feet, U. Jura of Colorado and Wyoming. *Scelidosaurus* Owen, L. Lias, England.

Tribe 3. **Ceratopsia**. Gigantic probably herbivorous, quadrupedal reptiles with a large skull, which carries a pair of horn-like processes in the frontal region just above the orbit and an unpaired process in the nasal



region. The parietals and squamosals project back over the neck as a shelf-like crest, the edge of which carries projections. There is a toothless *rostral* bone in front of the premaxilla, and a predentary, also edentulous, on the mandible. Small supra-temporal fossae are present, but no lateral-temporal. All the bones are solid. The teeth with forked roots and crushing crowns are borne by the maxilla and dentary. The fore-limbs are a little shorter than the posterior and have five hoofed digits. The sacrum is reinforced by adjacent lumbar and caudal vertebrae, and the ilium is extended antero-posteriorly. The pubis is directed forwards and meets its fellow; there is no postpubis. The astragalus is fused with the tibia. There are three hoofed toes. A dermal armour appears to have been present. They are known from the Cretaceous of Europe (fragments) and N. America. *Triceratops* Marsh (Fig. 214), skull 7 feet long, larger than in any other known land animal; body 20 feet. Upper Cretaceous of Wyoming; *Sterrhophilus* Marsh.

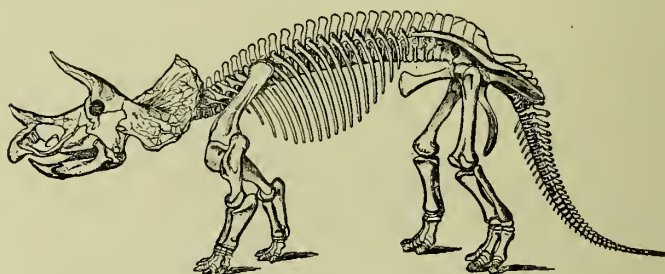


FIG. 214.—*Triceratops prorsus*  $\times \frac{1}{50}$  (after Marsh).

## Sub-class 5. PTEROSAURIA.

*With a superior and inferior temporal arcade, a fixed quadrate, and thecodont dentition; without pineal foramen. The fore-limbs are adapted for flight and the bones are hollow.*

The Pterosauria, or Pterodactyls, as they are sometimes called, were flying reptiles the remains of which are found in the Mesozoic rocks from the Lower Lias to the Cretaceous. In their external appearance and habit of life they present great resemblances to birds, but in the absence of feathers and the structure of the skeleton they differ considerably from these animals. They possess an elongated head which is set on the neck at a right angle, a long neck composed of elongated vertebrae, a very large anterior limb, the ulnar digit of which is enormously elongated to form the support of a patagial expansion of the integument (Figs. 215, 216), and a keeled sternum. Moreover the bones are hollow, and casts of the skull which have been obtained in one or two cases show that the brain possessed a large cerebellum extending forwards to the well-developed cerebral hemispheres and pushing apart the large optic lobes. There is evidence also of flocculi on the cerebellum.

The vertebral column is divided into cervical, dorsal, sacral and caudal regions, with about seven, fifteen, three to five and ten to forty vertebrae respectively. The precaudal vertebrae are procoelous the caudal amphicoelous. The cervical and anterior dorsal ribs are two-headed. The



sternum has a keel and there is no clavicle. The skull is rounded and bird-like. The occipital condyle is single and on the base of the skull. The cranial bones ankylose early as in birds, the orbits are large and with



FIG. 215.—*Dimorphodon macronyx* restoration  $\times \frac{1}{2}$ , L. Lias (after Owen, from Woodward)  
a antorbital fossa; n external nares; o orbit.

sclerotic plates, and there is a wide antorbital fossa as in Aves and Dinosauria. There is a postfrontal, and both upper and lower temporal arcades are present. Teeth are frequently present (on the margins of the jaws only),

but some genera are without them, in which case the jaws may have possessed horny beaks. The quadrates slope forward. The pterygoids enclose an interpterygoid vacuity and extend forwards to the vomers between the palatines.

The shoulder girdle is avine, and in some of the larger forms the scapula is attached to some of the dorsal vertebrae. The hand has four separate metacarpals and four digits (probably 1-4) of which the first three are clawed, the last enormously elongated and without a claw. The phalangeal formula is 2. 3. 4. 4. A splint-like bone is sometimes attached to the radial side of the carpus.

The pelvis is small and not at all avine. The ilia are expanded antero-posteriorly, and the ventral part consists of broad ischia meeting in a ventral symphysis and pierced by a small foramen. The pubis is separate and excluded from the acetabulum (as in crocodiles). The fibula is small and splint-like. There are two proximal and two distal tarsals, of which the proximal are sometimes fused with the tibia. The pes possesses five separate toes, of which four bear claws. The fifth digit is often shorter than the rest and is sometimes divaricated from them as

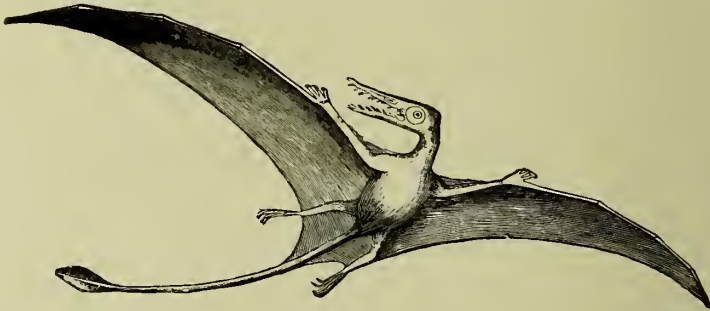


FIG. 216.—*Rhamphorhynchus phyllurus* restored by Marsh  $\times \frac{1}{2}$ . U. Jura (from Woodward).

though it assisted in the support of the patagium. There was no dermal armour, but abdominal ribs were present.

From this account it is clear that the Pterosauria resemble birds in the structure of the shoulder girdle, in certain features of the skull, but they differ from them completely in the structure of the organ of flight and of the limbs, in the presence of postfrontal bones, and of both temporal arcades in the skull, and in the structure of the vertebral column and pelvis.

They make their appearance in the Lower Lias, and the earliest known genus *Dimorphodon* (Fig. 215) presents all the features of specialisation of the group.

*Dimorphodon* Owen (Fig. 215) with teeth and long tail, Lower Lias, England. *Rhamphorhynchus* v. Meyr (Fig. 216) with teeth and long tail, U. Jura (Lithographic Slate). *Pterodactylus* Cuvier, with teeth, tail short, Lithographic Slate. *Pteranodon* Marsh, contains the largest form (skull to 2 feet, wing spread to 20 feet), without teeth, tail short, Cretaceous, U. S. *Ornithochirus* Seeley, similar to last but with teeth, Cambridge Greensand.

Sub-class 6. ICHTHYOSAURIA.

*Very peculiar large extinct fish-like marine reptiles with biconcave vertebrae, four paddle-shaped limbs with very short long-bones ; a large number of phalanges and often more digits than five, with pineal foramen, pterygoids reaching forward to the vomers, and fixed quadrate. Trias to Cretaceous.*

The *Ichthyosauria* were large fish-like reptiles, which inhabited the seas of a considerable part of the earth during the secondary period. Their remains are found in Europe, Africa, America, Australia, New Zealand, and India. Some of the larger kinds appear to have reached a length of from 30 to 40 feet. They are distinguished externally by the large size of the head and of the eyes (Fig. 217), by the absence of a neck, by the two pairs of flipper-like appendages, by the dorsal median fins, and by the vertical caudal fin, into the lower lobe of which the vertebral

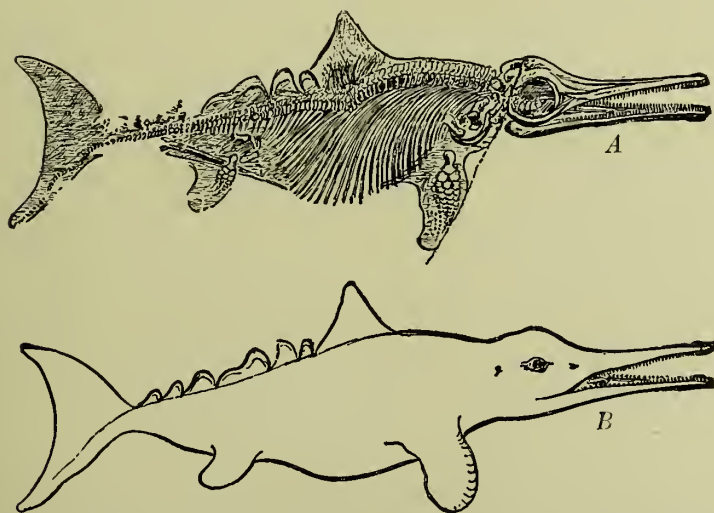


FIG. 217.—*Ichthyosaurus quadriscissus*. A Fossilised skeleton. B Outline restoration showing integument with dorsal and caudal fins. L. Jurassic (U. Lias), Württemberg (after E. Fraas, from Woodward).

column is prolonged. The size and form of the head, the absence of the neck and the form of the anterior limb give them a certain superficial resemblance to whales. They have indeed been spoken of as the whales of the Mesozoic seas. That they are true reptiles must be considered certain ; but they stand far apart from other reptiles and cannot be said to show resemblances to one sub-class more than to another. By the presence of a pineal foramen in the roof of the skull and the form of the pectoral girdle they resemble the lizard group ; by the anterior extension of the pterygoid to the vomers, the *Rhynchocephalia* ; and by the form of the temporal arcade they recall the *Anomodontia* and *Chelonina*.

In the zoological language of the day this isolation in structure with regard to other reptiles is expressed by saying that their descent is unknown ; but in this they do not differ from other reptilian groups, of none of which

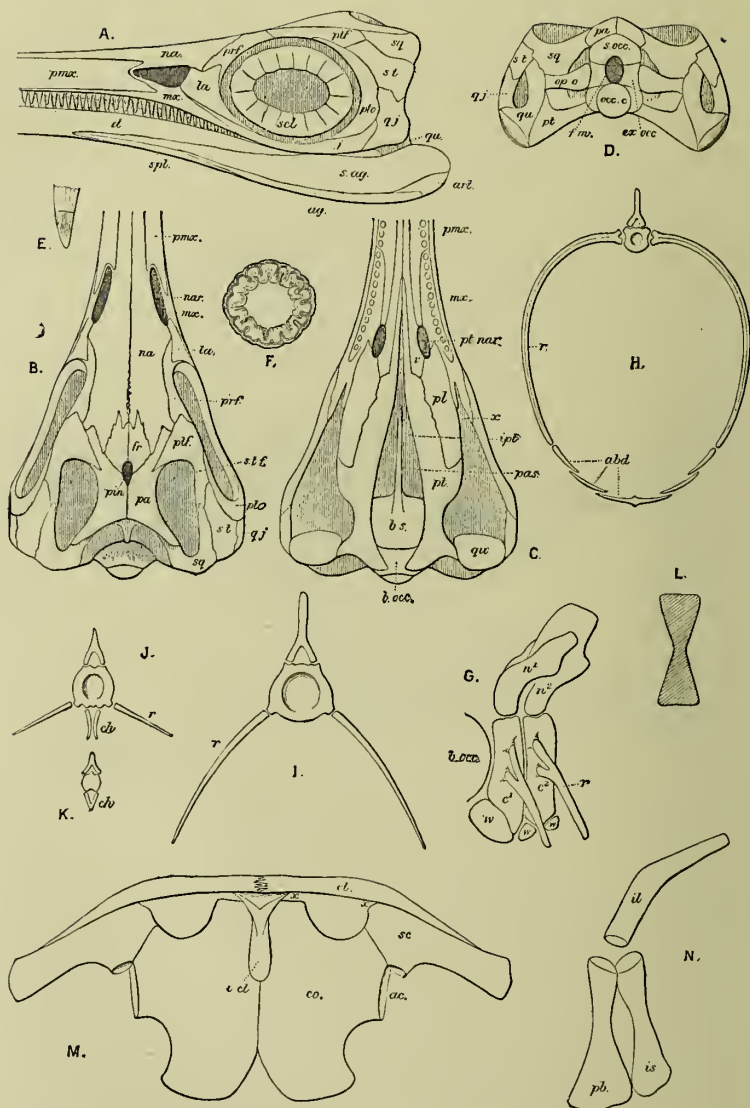


FIG. 218.—Diagrams illustrating the principal characters of *Ichthyosaurus* (from S. Woodward). A side, B dorsal, C ventral, D posterior view of the skull of *Ichthyosaurus longifrons*, L. Jurassic (U. Lias). *ag* angular; *art* articular; *b.occ* basioccipital; *b.s* basisphenoid; *d* dentary; *ex.occ* exoccipital; *f.m.* foramen magnum; *fr* frontal; *i.pt* interpterygoid vacuity; *j* jugal; *la* lacrymal; *mx* maxilla; *na* nasal; *nar* external nares; *occ.c* occipital condyle; *op.o* opisthotic; *pa* parietal; *pas* parasphenoid; *pin* pineal (parietal) foramen; *pt* palatine; *pmx* premaxilla; *prf* prefrontal; *pt* pterygoid; *pt.f* postfrontal; *pt.nar* posterior nares; *pto* postorbital; *qj* quadratojugal; *qu* quadrate; *s.ag* surangular; *sc* sclerotic plates; *s.occ* supraoccipital; *spl* splenial; *sq* squamosal; *s.t* supratemporal (prosquamal); *s.t.f*

supratemporal vacuity; *x* space for ectopterygoid (?); *v* vomer. Restored from specimen in British Museum.

*E* Upper tooth of *Ichthyosaurus communis* showing enamelled crown and fluted base,  $\times \frac{1}{2}$  (L. Lias).

*F* transverse section of base of tooth.

*G* atlas and axis of *Ichthyosaurus longirostris*, U. Lias. *b*. occipital condyle of skull; *c'* centrum of atlas; *c''* centrum of axis; *n'* paired neural arch of atlas; *n''* single neural arch of axis; *r* ribs; *w* subvertebral wedge-bones (hypocentra) (after Owen).

*H* dorsal vertebra and ribs of *Ichthyosaurus*, anterior aspect, L. Lias. *abd* abdominal rib; *r* rib (after Owen).

*I, J, K* vertebra from base of tail and two caudals of *Ichthyosaurus*, anterior aspect. *ch*. chevron bone; *r* rib (after Owen).

*L* section of caudal vertebra of *Ichthyosaurus*.

*M* ventral view of pectoral girdle of *Ichthyosaurus* (restored from specimen in Brit. Mus.). *ac* glenoid cavity; *cl* clavicle; *co* coracoid; *i.cl* interclavicle; *sc* scapula; *x* edges originally bordered by cartilage.

*N*. Outer aspect of left pelvic arch of *Ichthyosaurus communis* (from specimen in Brit. Mus.). *il* ilium; *is* ischium; *pb* pubis.

can it be said that the descent is even approximately known. The progress of palaeontological research has made known to us the immense variety which has characterised the organisation of reptiles, but it is at the same time rendering more difficult the elucidation of pedigrees. For the greater the variety in organisation that is revealed to us, the more involved become the interrelationships between the different groups.

The skull (Fig. 218 A-D) has a long rostrum which consists almost entirely of the premaxillae. The maxillae are small and the anterior nares are placed far back just in front of the large orbits. The teeth which are conical and crocodilian are placed in a continuous groove (rarely in separate pits) on the premaxillae, maxillae and mandibles. They sometimes show a folding of the enamel as in Labyrinthodonts. The eye has a circle of bony sclerotic plates and the orbit is closed behind by the post-frontal, postorbital, and jugal. There is a single broad temporal arcade which consists of squamosal, supratemporal (prosquamosal) and quadrato-jugal, and corresponds to the superior and inferior temporal arcades of *Rhynchocephalia* etc., the lateral temporal fossa being closed. There is a supratemporal fossa bounded by the parietal, squamosal and post-frontal. The nasals are large, the parietals and frontals are small and paired; there is a large pineal foramen between the parietals and frontals. All the occipital bones are present and separate, as are the opisthotic and prootic. The single occipital condyle is formed by the basioccipital alone. There is a basisphenoid, but alisphenoids, presphenoid and orbitosphenoids are absent. There is said to be an epipterygoid reaching from the pterygoid to the prefrontal. A median splint extends forwards from the basisphenoid in the vacuity between the pterygoids; this may be called the parasphenoid or basisphenoidal rostrum. The pterygoids are large and widely separate except in front where they touch; behind they join the basisphenoid and quadrate, and extend anteriorly between the palatines to the vomers. The internal nares are between the vomers on the inside and the maxillae and palatines on the outside. The quadrate is fixed. The mandible is long and narrow and without a coronoid process. The hyoid appears to be represented by a pair of stout, rib-like bones beneath the pterygoids.

The vertebrae (Fig. 218 G-L) are very numerous, 150 or more in number, of which 100 are caudal. They are divisible into caudal and precaudal only. The centra are amphicoelous and very short anteroposteriorly. The neural arches are separate from the centrum and the zygapophyses are feeble and sometimes even absent. The centra possess on each side two short lateral processes, to which the double headed ribs are attached.



The atlas and axis vertebrae (*G*) are usually fused together and possess three wedgelike hypocentra, one in front of the atlas, the next between the atlas and axis, and the third behind the axis. Chevron bones are found on the caudal vertebrae but their halves generally remain separate. The hind end of the vertebral column is bent ventralwards into the ventral lobe of the caudal fin. Abdominal ribs are present consisting of a median piece and two or three lateral pieces on each side (Fig. 218 *H*). There is no bony sternum. The shoulder girdle is lizard-like and very strong; it is shown in Fig. 218 *M*. The pelvic girdle is feeble (Fig. 218 *N*); all the bones join in the acetabulum, but the ilia are not attached to the vertebral column and it is doubtful if there was a pubic or ischiadic symphysis.

The skeleton of the limbs is highly peculiar (Fig. 219). The long bones (humerus, femur, radius, ulna, tibia, fibula, metacarpals) are all much shortened, sometimes broader than long. Moreover the phalanges are very numerous and the digits sometimes appear to be more than five (to eight or nine). This is caused

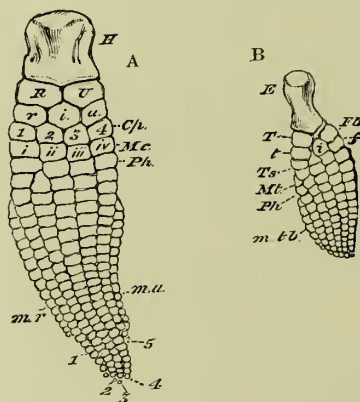


FIG. 219.—*A* anterior, *B* posterior limb of *Ichthyosaurus intermedius* (after Huxley). *Cp.* carpalia; *E* femur; *f* fibulare; *Fb* fibula; *H* humerus; *i* intermedium; *Mc* metacarpals; *m.r* extra radial digit; *Mt* metatarsals; *m.tb* extra tibial digit; *m.u* extra ulnar digit; *Ph* phalanges; *R* radius; *T* tibia; *t* tibiale; *Ts* tarsalia; *U* ulna; 1, 2, 3, 4, 5 digits.

partly by bifurcation of some of the digits and partly by the presence of an additional row of phalanges on the preaxial and postaxial side of the manus and pes (*m.r*, *m.u*, *m.tb*). The carpalia of the distal row are three or five, and the number of digits is said to vary from three to five, but this is not allowing for the extra rows of phalanges above referred to. It is important to notice that the relatively large size of the manus and pes (as compared with the rest of the limb) is obtained not by an increase in length of the phalanges but by an increase in their number. This is a peculiarity of the *Ichthyosauria* which is met with to a very small extent if at all in other reptiles or in mammals. The apparent increase in the number of the digits as indicated by the

number of rows of phalanges is a most remarkable feature met with in no other pentadactyle form. Whether it is to be regarded as a polydactyle condition such as must have existed in forms connecting the piscine with the pentadactyle type is uncertain; no remains of animals with such intermediate types of limbs being known to us. The skin appears to have been leathery and without scales or dermal plates.

That the *Ichthyosauria* were viviparous appears to be indicated by the fact that specimens of them are found containing the remains of fair sized young individuals in what must have been the abdominal cavity. Their coprolites are known and they contain scales and bones of fishes and fragments of *Cephalopoda*. The coprolites also show indications of having passed through an intestine with a spiral valve.

There is very little variation in structure in the species known to us.

They are all placed in one family and in about four to six genera. Considering the great abundance of individuals as indicated by the frequency with which their remains are found, this is a remarkable fact.

In *Mixosaurus* Baur, the genus to which all the Triassic remains are assigned, the teeth are more variable in size, and the limbs are less paddle-shaped, the radius and ulna being longer than broad and having a small space between them. *Shastasaurus* Merr. from the Upper Trias of California may possibly belong to this genus. *Ichthyosaurus* König is the typical and most common genus. It is most common in the Lias but extends into the Cretaceous. *Ophthalmosaurus* Seeley is edentulous or almost so, and the carpal and metacarpal bones and phalanges are round and not pressed together as in the preceding genera; Upper Jurassic and Cretaceous of England. *Baptanodon* Marsh is completely edentulous, possibly belongs to the last named genus, Jurassic of Wyoming. It is quite clear from this small amount of diversity of structure that we are acquainted with but a minute fraction of the group. There must have been, possibly in Triassic and earlier times, an immense number of forms the remains of which have yet to be discovered, and which may, when they are discovered, enable us to relate these isolated creatures to other reptilian groups.

#### Sub-class 7. PLESIOSAURIA.\*

*Amphibious or marine lizard-like reptiles with long neck, two pairs of five-toed limbs, and strongly developed pectoral and pelvic girdles. The skull has a supratemporal fossa only, a single broad temporal arcade, large pterygoids which reach the vomers and meet in the middle line, fixed quadrates, and a pineal foramen. Triassic to Cretaceous of Europe, N. and S. America, N. Zealand, and India.*

In the triassic forms the limbs appear to have been less modified than in the post-triassic and to have been adapted for walking. In the post-triassic forms they are paddle-like and provided with an increased number of phalanges though not of digits. The larger species may attain a length of 40 feet. The vertebrae are weakly biconcave or flat, and the neural arches are usually suturally united to the centra. The number of cervical vertebrae is always great (20 to 40) and the tail, especially in the marine forms, is short. All the vertebrae carry ribs except the atlas and the axis and the hinder caudals. The cervical ribs are articulated to an articular surface on the centra alone; they are two-headed in the earlier genera, single-headed in the later forms. In the trunk the ribs are one-headed and articulated to a transverse process of the neural arch or more rarely directly to the neural arch. There are two to four sacral vertebrae, which are not fused. The caudal vertebrae have chevrons, and their ribs are articulated to the centrum.

The features of the skull are clearly shown in the diagrams (Fig. 220) illustrating the skull of *Plesiosaurus*. The premaxillae are large and form the short rostrum. The anterior nares are near the orbit. The orbit is closed behind by the jugal and a bone which corresponds to the post-orbital and postfrontal. There are large supratemporal fossae, and the temporal arcade is formed by the backward continuation of the jugal and of the bone which is supposed to consist of postfrontal and post-

\* Called by Owen *Sauropterygia*.

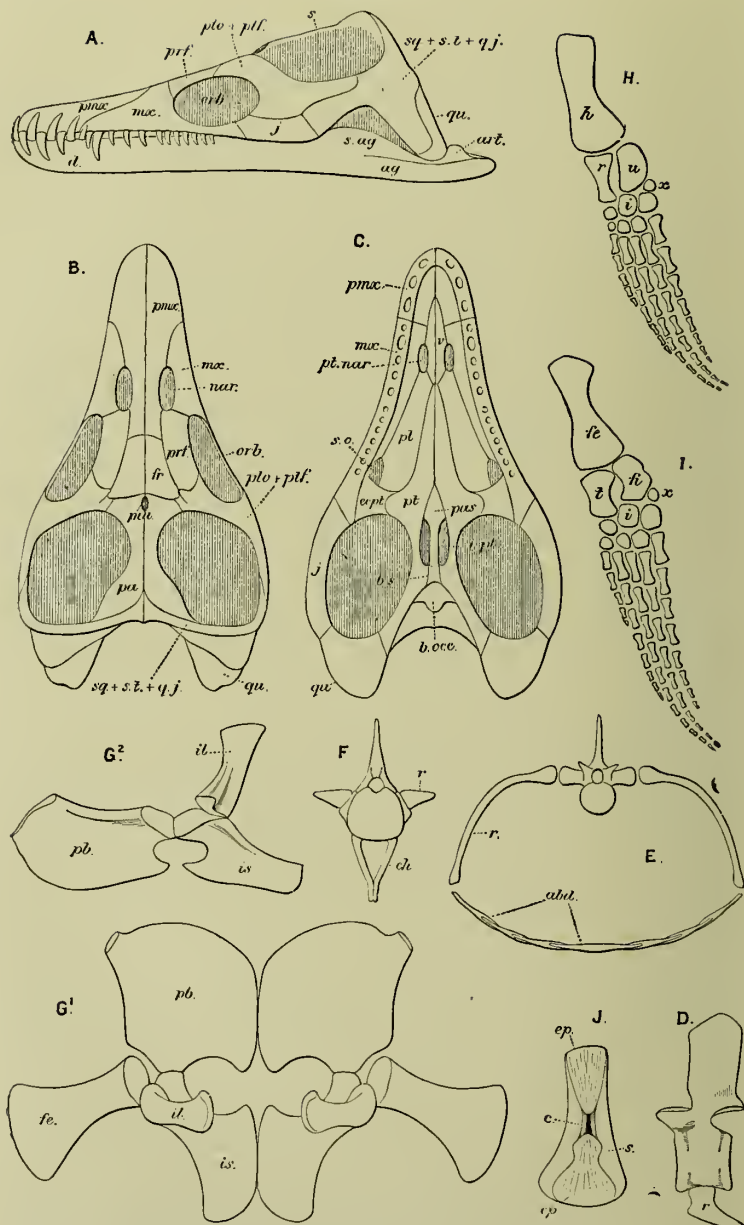


FIG. 220.—Diagram illustrating the principal characters of the Plesiosauria (from S. Woodward).

A, B, C Lateral, dorsal, and ventral view of the skull of *Plesiosaurus macrocephalus*  $\times \frac{1}{2}$ ,

L. Lias (modified after C. W. Andrews). *ag* angular; *art* articular; *b.occ* basioccipital; *bs* basisphenoid; *d* dentary; *cept* ectopterygoid (transpalatine); *fr* frontal; *i.pt* interpterygoid vacuity; *j* jugal; *mx* maxilla; *nar* external nares; *orb* orbit; *pa* parietal; *pas* parasphenoid; *pin* pineal foramen; *pl* palatine; *pmx* premaxilla; *prf* prefrontal; *pt* pterygoid; *pt.f* postfrontal; *pt.nar* internal nares; *pto* postorbital; *qj* quadratojugal; *qu* quadrate; *s* supratemporal vacuity; *s.ag* surangular; *so* suborbital vacuity; *st* supratemporal (prosquamosal); *sq* squamosal; *v* vomer.

*D Plesiosaurus dolichodirus*; cervical vertebra, left side;  $\times \frac{1}{4}$ . L. Lias. *r* rib.

*E Cryptoclidus oxoniensis*, transverse section of abdomen of immature specimen,  $\times \frac{1}{10}$ .

U. Jurassic. *abd* abdominal ribs; *r* rib.

*F. Plesiosaurus dolichodirus*; caudal vertebra, anterior end,  $\times \frac{1}{4}$ , L. Lias; *ch* chevron bone; *r* rib.

*G<sup>1</sup>* dorsal, *G<sup>2</sup>* side view of pelvis of *Muraenosaurus leedsi*,  $\times \frac{1}{14}$ , Oxford Clay (after C. W. Andrews). *fe* femur; *il* ilium; *is* ischium; *pb* pubis.

*H* pectoral, *I* pelvic limbs of the same specimen of *Plesiosaurus dolichodirus*,  $\times \frac{1}{15}$ , L. Lias (Brit. Mus.). *fe* femur; *fb* fibula; *h* humerus; *i* intermedium; *r* radius; *t* tibia; *u* ulna; *x* pisiform.

*J* humerus or femur of Plesiosaurian in median longitudinal section,  $\times \frac{1}{15}$ , U. Jurassic. *c* central cavity; *ep* epiphyses; *s* shaft. (Brit. Mus.)

orbital, to meet a large bone which overlaps the fixed quadrate and is supposed to be equivalent to the supratemporal, squamosal and quadratojugal. There is a pineal foramen. The internal nares are between the vomers and the maxillae. The palatines are separated by the pterygoids which touch for the greater part of their length, but are separated by an interpterygoid vacuity behind. In the middle of the latter is the basisphenoidal rostrum. In the triassic genera the pterygoids are in contact throughout. The occipital condyle is single and mainly formed by the basioccipital. Sclerotic plates have not been observed. The dentition is thecodont and teeth are borne by the premaxillae, maxillae and mandible, and occasionally in the triassic genera by the pterygoids.

In the triassic genera the pectoral girdle is on the ordinary reptilian type, except that the coracoids meet in a ventral symphysis and there is no sternum preserved. In the post-triassic forms however the pectoral girdle presents some remarkable features. The symphysis of the coracoids is much prolonged anteroposteriorly and the scapulae extend ventrally towards each other, so as nearly or completely to meet in the median ventral line in front of the coracoids. At the same time the clavicles and interclavicle become reduced.

The pelvic girdle is well developed (Fig. 220 *G*). The ilia articulate with the ribs of the sacral vertebrae and all three bones enter into the acetabulum, but the ilium joins the ischium only. There is a pubic and an ischiadic symphysis. The limbs are more elongated and leg-like in the triassic genera and have the normal number of phalanges, but in the later forms they are more paddle-like and the bones of the fore-arm and fore-leg shortened, and the phalanges are more numerous.

Numerous close-set abdominal ribs are present, and the skin appears to have been without scales and dermal plates. Vertical fins have not been certainly made out.

Fam. 1. **Nothosauridae.** Triassic Plesiosaurs with elongated limbs adapted for moving on land as well as in water. The palate is without an interpterygoid vacuity. There are about 20 cervical vertebrae and the cervical ribs are double-headed. The number of phalanges in both limbs is normal. The coracoidal symphysis is not much extended longitudinally, and the clavicles are well developed. *Lariosaurus* Curioni, Triassic shales of Lake Como; *Pachypleura* Cornalia (*Neusticosaurus* Sceleý) U. Trias, Lombardy etc.; *Dactylosaurus* Gürich. *Anarosaurus* Dames, *Cymatosaurus* Dames, Muschelkalk, Silesia and Thuringia; *Pistosaurus*, *Simosaurus* v. Meyer, Muschelkalk; *Nothosaurus* Münster, Muschelkalk, Germany



and France. *Mesosaurus* (p. 334) is supposed by some authors to belong here.

Fam. 2. **Plesiosauridae.** The limbs are paddle-shaped and adapted for swimming; the radius and ulna and tibia and fibula are shortened, and the number of phalanges, which are elongated, is increased. An interpterygoid vacuity is present in the palate. An epipterygoid is present. The neck is long with 30 to 40 cervical vertebrae. The cervical ribs are single- or double-headed. The coracoid symphysis is much extended antero-posteriorly and the scapulae tend to meet in a median ventral symphysis. *Plesiosaurus* Conybeare, Lias of England and Germany. *Eretmosaurus* Seeley, L. Lias, England. *Rhomaleosaurus*, *Colymbosaurus*, *Muraenosaurus* Seeley, U. Jurassic, England. *Cryptoclidus* Seeley, all ribs single-headed, U. Jurassic, England. A number of diverse genera from the U. Cretaceous of N. and S. America and N. Zealand. *Pliosaurus* Owen, with relatively large head and short neck (20 vertebrae), Lias to U. Jurassic, England, Europe, India. *Megalneusaurus* Knight, largest known Plesiosaur, U. Jurassic, Wyoming, U.S. *Elasmosaurus* Cope, U. Cretaceous, Kansas, U.S. *Polyptychodon* Owen, M. and U., Cretaceous, England, Germany, Russia.

### Sub-class 8. ANOMODONTIA.\*

*Terrestrial reptiles with limbs adapted for the support of the body, with biconcave vertebrae, fixed often reduced quadrate, and pineal foramen. The temporal fossa is completely closed by the bones of the temporal region or there is a broad temporal arcade. The bones of the pectoral and pelvic girdles are fused or immovably connected by suture. Permian and Triassic formations of Europe, N. America, S. Africa, and India.*

The Anomodontia form a somewhat diverse group of apparently terrestrial reptiles. They are known by remains which are in most cases imperfect, and it is highly probable that the sub-class will eventually have to be broken up. The group however as it stands combines a number of reptilian features not found together in any other reptilian sub-class with some highly remarkable mammalian characteristics. Of their essentially reptilian features, we may mention the pineal foramen, the quadrate, the compound mandible, the general presence of pre- and post-frontals. To show the peculiar combination of characters found in no other reptilian group, we may draw attention to the union of the upper and lower temporal arcades into one broad arcade, unpierced as a rule by a lateral temporal fossa and found elsewhere only in Plesiosauria and Ichthyosauria; to the frequent presence of a secondary palate, which recalls that of the Chelonia; to the thecodont dentition which is found also in Plesiosauria, but not in the two other groups; to the structure of the pelvis which is quite different from that of any of the three above-mentioned groups; and to the absence of abdominal ribs.

The mammalian characters are however those which preeminently distinguish them from other reptiles. These are: the frequent differentiation of the teeth into incisors, canines and molars (Fig. 222); the resemblance of the single temporal arcade to the mammalian zygomatic arch; the mammalian character of the limbs which carry the body high above the ground (Fig. 221); the union of the pelvic bones into an os innominatum (Fig. 221); and the continuity of the pubic and ischiadic symphysis;

\* Sometimes called *Theromorpha*.



the shape and frequent presence of a spine on the scapula, and many features of the limb bones in the different sub-orders, e.g. fore-limb of *Theriodesmus*. Moreover the squamosal often descends far down outside the quadrate (Fig. 223), and may contribute to the articular surface for the lower jaw.

The vertebrae are amphicoelous and the cervical ribs are double-headed. Hypocentra are either much reduced or absent. Abdominal ribs are never found. The skull has a well-marked supra-temporal fossa (except in the *Pareiasauria*), and in one or two forms the temporal arcade is perforated by a small aperture recalling the lateral temporal fossa. The quadrate is fixed and frequently reduced in size. Secondary palatal plates of the premaxillae, maxillae and palatines appear to be developed in many forms. The pterygoids are large, extend back to the quadrates and meet in the middle line. The occipital condyle is single or trifold, or double (*Cynognathus*). The mandible usually shows a composition of several bones, but this cannot always be seen. Pre- and post-frontals can usually be made out, but sometimes, in consequence of the absence of sutures, they are indistinguishable. In the pectoral arch there are clavicles, interclavicle and ossified epicoracoids; the scapula is frequently mammalian and has a spine and all the bones are immoveably united. The pelvic girdle is thoroughly mammalian; all the bones are immoveably united and there are two obturator foramina. The limbs are not well known; but they appear to have been stout pentadactyle structures.

From the above short description and from the subjoined account of their orders it is clear that the *Anomodontia* present both reptilian and mammalian features. Which of these preponderate it is difficult to say.\* By most investigators they are regarded as reptiles, and there is undoubtedly much to be said for this view, which has been followed in the present work; but it must not be forgotten that our knowledge of even the coarser features of their skeleton is very imperfect, and that we know nothing of the finer details or of the soft parts. On the whole we think that there is much to be said for the view that the *Anomodontia* are neither reptiles nor mammals, but that they represent an independent type of structure, we will not say intermediate between these two, but combining features belonging to each. There is no reason that we can see for regarding them as ancestral to mammals, and we do not propose to consider the matter from that point of view. Having regard to the extreme incompleteness of our knowledge of their anatomy such a discussion would hardly be profitable, and might draw off our attention from wider problems of evolution which are perhaps more ripe for settlement. There are two additional facts with regard to this group which must be borne in mind. In the first place they are almost the only purely terrestrial extinct reptiles known, and in the second they are known to us in a very large number of cases by their skull only.

#### Order 1. PAREIASAURIA.

The temporal fossa is completely covered over dorsally by bone. There may be a small latéro-temporal fossa. Teeth conical or with a compressed, cuspidate crown; those on the margin of the jaws in a uniform series. Pineal foramen large. Vertebral centra pierced for the persistent notochord. Permian and Triassic.

\* See the "Discussion on the origin of Mammals" in the Proceedings of the *Fourth International Congress of Zoology*, Cambridge, 1899.

*Pareiasaurus* Owen (Fig. 221), heavy, massive creatures to 8 feet long, with stout limbs, short tail; bones of skull roughly sculptured; bones of the palate not suturally separated, with rows of small teeth, with interpterygoid vacuity; occipital condyle single; the mandibular elements are not separated by sutures; 18 presacral vertebrae, 4 sacral not fused, about 30 caudal with chevrons, all except the posterior caudal with single-headed ribs attached to facets on the vertebrae; wedge-shaped hypocentra between the dorsal vertebrae; the scapula slopes backwards and possesses a longitudinal spine; acetabulum closed; limbs plantigrade with 5 digits with claws, hind limbs larger than front; sternum and abdominal ribs unknown; Karoo sandstone, S. Africa. *Elginia* Newton, known only by the skull with spikes and horn-like projections, triassic sandstones of Elgin. *Procolophon* Owen, a small animal the skull of which shows the sutures; there is a small lateral temporal fossa and small teeth on the pterygoid and vomer; Karoo sandstone, S. Africa. *Aristo-desmus* Seeley, L. Trias, Switzerland. *Otocoelus* Cope, with a dorsal carapace of 12 or more transversely extended bars of bone, Permian Texas; and other genera.

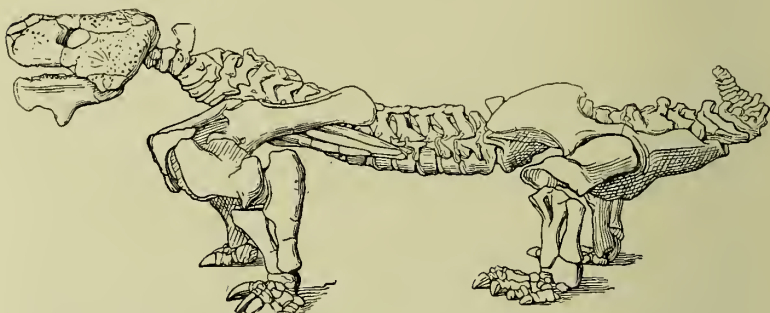


FIG. 221.—Skeleton of *Pareiasaurus* (*Pareiasaurus*) *bairdi* Seeley. Karoo Sandstone, Cape Colony (after Seeley from Woodward).

## Order 2. THERIODONTIA.

There is a single broad temporal arcade with a large superior and sometimes a small lateral temporal fossa; the quadrate is small, the occipital condyle bilobed; palatal plates are developed by the maxillae and sometimes by the palatines; the marginal teeth of the jaws are differentiated into incisors, canines and molars; teeth are almost always limited to the dentaries, maxillaries and premaxillaries; the external bones of the skull are not sculptured; the scapula has a mammal-like spine, but the skeleton of the trunk and the appendages is imperfectly known: all from the Karoo sandstone of S. Africa, but there are remains from the Permian of the U.S.A. and of Russia, which may belong here.

*Galesaurus* Owen, known only by the skull, dentition  $i \frac{4, 4}{4, 4} c \frac{1, 1}{1, 1}$  and an undetermined number of molars laterally compressed and in part tricuspidate. *Lycosaurus* Owen, skull only known; *Aelurosaurus* Owen, known only by skull; *Cynognathus* Seeley, vertebral column and limb arches found with skull; skull (Fig. 222) very mammalian; vertebrae amphicoelous; dentition  $i \frac{4}{3} c \frac{1}{1} m \frac{9}{9}$ , molars triconodont.

The following genera with broad molar-like teeth have been united by Seeley into a special order, the *Gomphodontia* :

*Tritylodon* Owen, with transversely expanded molar-like teeth and a pair of large incisors probably growing from persistent pulps ; with a secondary palate and reduced quadrate ; very mammal-like, known by skull only ; molars multituberculate. *Diademodon* Seeley, *Trirachodon* Seeley, both with multituberculate teeth. *Theriodesmus* Seeley, known by a remarkably mammalian fore-limb and manus ; and other genera. All the above are from S. Africa. *Triglyphus* Fraas, known only by its molar-like teeth is from the U. Trias, Stuttgart.

The following known from imperfect remains from the Permian of Russia are probably *Theriodontia* ; *Deuterosaurus* Eichw., *Rhopalodon* Fischer, with lanceolate molars and sclerotic ring.

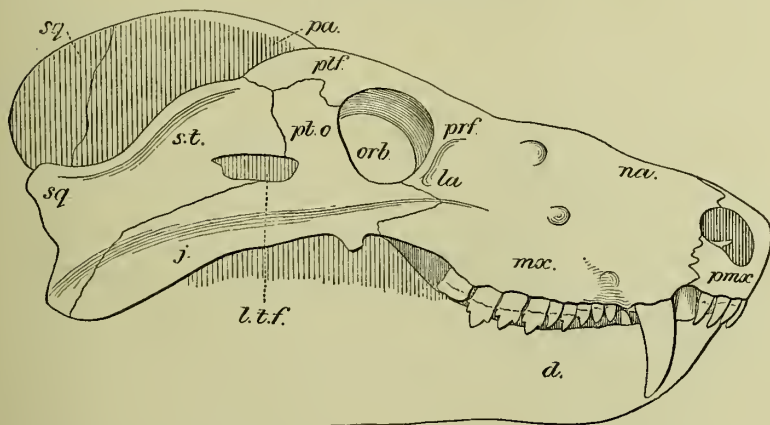


FIG. 222.—*Cynognathus craternotus*, right side of skull with imperfect mandible (after Woodward slightly restored). The molars possibly project further than in life and the crown of the last is broken. *d* dentary ; *j* jugal ; *l.t.f.* small lateral temporal vacuity ; *la* lacrymal ; *mx* maxilla ; *na* nasal ; *orb* orbit ; *pa* parietal ; *pmx* premaxilla ; *prf* prefrontal ; *pt.o* postorbital ; *ptf* postfrontal ; *st* supratemporal ; *sq* squamosal.

### Order 3. DICYNODONTIA.

Highly specialised land-forms, known by fragments from the Trias of S. Africa, East India, the Urals, and Scotland. There is a single temporal arcade formed mainly by the squamosal which is very large and lies over the small quadrate (Fig. 223). The jaws are edentulous except for the occasional presence of a pair of tusk-like teeth in the maxillae growing from persistent pulps. There do not appear to be any secondary palatal plates and the pterygoids are large, meeting in front of the basisphenoid. The cervical ribs are double-headed, the dorsal single-headed ; the vertebral column consists of 7 to 8 cervical, 12 to 13 dorsal, 5 to 6 fused sacral and about 20 caudal vertebrae. There appears to be a pineal foramen. The scapula has an acromion, the pelvic bones are fused into an os innominatum.

*Dicynodon* Owen, *Oudenodon* Owen, *Ptychognathus* Owen, Karoo Sandstone of S. Africa. *Gordonia* and *Geikia* Newton, Elgin Sandstone Scotland ; etc.

## Order 4. PLACODONTIA.

Known by their skulls only from the Middle Trias (Muschelkalk) of Germany and Russia. With very peculiar dentition of large pavement-like crushing teeth on the jaws and palate, which seem to indicate that they probably lived on hard-shelled molluscs. The skull recalls that of Diconodonts. *Placodus* Agassiz; *Cyamodus* v. Meyer.

## Sub-class 9. CHELONIA.\*

*Body encased in a bony capsule, jaws without teeth but with horny beaks, nasal opening single and at the front end of the snout, quadrate immovable and appendages with five digits. The lower temporal arcade alone is present. Anal opening round or longitudinal.*

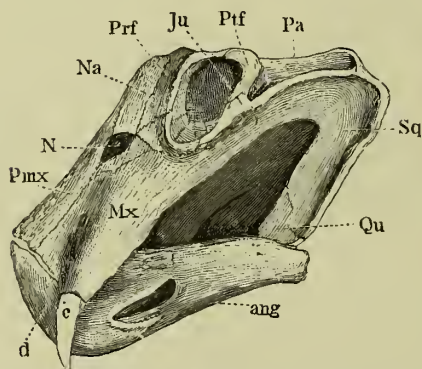


FIG. 223.—*Ptychognathus declivis* Owen, Karoo Sandstone. Side view of skull (from Zittel after Owen). *ang* angular, *c* maxillary tusk, *d* dentary, *Ju* jugal, *Mx* maxilla, *N* external narial opening, *Na* nasal, *Pa* parietal, *Pmx* premaxilla, *Prf* prefrontal, *Ptf* postfrontal, *Qu* quadrate, *Sq* squamosal.

No other group of Reptiles is so clearly defined and characterised to the same extent by peculiarities of form and organisation as is that of the *Chelonia*, and this applies to the extinct as well as to the living forms. The investment of the body by a shell composed of an upper, more or less arched osseous plate (*carapace*), and by a lower ventral plate (*plastron*) forms a character

as distinctive of the Chelonia, as is the possession of wings and feathers of the class Aves. This shell is covered, except in the

\* A. Bojanus, "*Anatome Testudinis Europae*," Vilnae, 1819. H. Rathke, "*Ueb. d. Entwick. der Schildkröten*," Braunschweig, 1848. L. Agassiz, "*Embryology of the Turtle*," *Contributions to the Natural History of the United States*, 1 and 2, Boston, 1857. A. Strauch, "*Chelonologische Studien*," *Mém. de l'Acad. St. Petersburg*, (7) 5, 1862. Gray & Sowerby, *Tortoises, Terrapins and Turtles drawn from life*, London, 1872. W. K. Parker, "*Development of the Green Turtle*," *Challenger Reports*, 1, 1880. J. E. Gray, "*Notes on the families and genera of Tortoises, and on characters of their skulls*," *Proc. Zool. Soc. London*, 12, 1869. Mitsukuri, *Contributions to the embryology of Reptilia*, *Journal Coll. Sci. Imp. Univ. Japan*, 4, 1890; 5, 6; 1893, 10, 1896. Th. Huxley, "*The Anatomy of Vertebrated Animals*," London, 1871. G. A. Boulenger, "*Catalogue of Chelonians in the British Museum*," London, 1889. Hoffmann, Gadow, Cope, Zittel, *op. cit.*



*Trionychoidea* and the *Athecae* in which the skin is soft, by a horny epidermal exoskeleton consisting of horny plates which constitute the so-called "tortoiseshell," and which have an arrangement roughly resembling that of the subjacent bony plates of the shell.

The carapace (Fig. 224), beneath which the head and tail can often be retracted, owes its origin to the formation of bony plates in the dermis, some of which become attached to the internal skeleton. Allowing for some variation in details, it is constituted as follows: there is a median row of usually eight *neural* plates, which are fused (Fig. 224)

to the spinous processes of eight of the thoracic vertebrae (2nd to 9th); in front of the first neural plate and suturally joined to it, is a large *nuchal* plate (Fig. 224, *Nu*), which lies over and is joined by ligament to the neural spine of the last (8th) cervical vertebra. Behind the eighth neural are the median *pygal* (*Py*) plates (one to three in number), of which the first two are united to the eighth costal (*C8*) and the last to

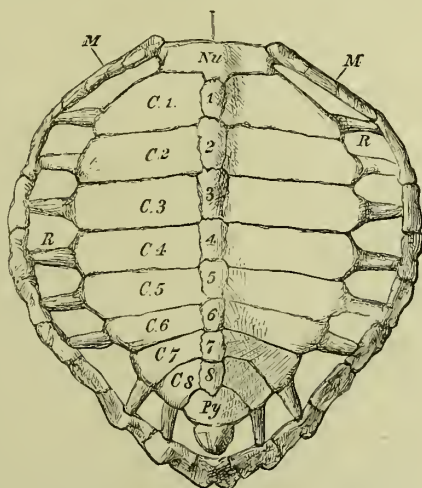


FIG. 224.—Dorsal view of the carapace of *Chelone midas* (from Huxley). *Nu* nuchal, *Py* pygal plates; *M* marginal plates; *R* ribs; 1-8 neural plates; C1-C8 costal plates.

the hinder marginal. The ribs of the second to the eighth thoracic vertebrae, distinguished from the first and last ribs by their greater length, are fused with the broad, transversely arranged costal plates of the carapace (*C*). The costal plates are joined with one another by sutures, and present the special peculiarity of giving off broad transverse plates, which arch over the muscles of the back and join the neural plates (Fig. 225). The ribs project beyond the costal plates and end, each of them, in one of the *marginal* plates (*M*), of which there are usually eleven pairs and a median posterior. The marginals form the boundary of the carapace. The first marginal on each side is



attached to the side of the nuchal, the last marginal is in the middle line and attached to the last pygal. Of these plates the nuchal, pygal, and marginal used to be considered as purely dermal structures, the neurals and costals being regarded as expansions of the internal skeleton.

The *plastron* (Fig. 226) or ventral part of the shell is attached directly or by ligament to the marginals and is quite separate from the internal skeleton. It consists, like the rest of the shell, of purely dermal bones, some of which lie behind and some in front of the umbilicus. It is therefore partly a thoracic and partly an abdominal structure. In the turtle it consists of nine pieces—a median *entoplastron* (interclavicle), and four paired pieces, the *epiplastra* (clavicles), the *hyoplastra*, the *hypoplastra* and the *xiphiplastron* (Fig. 226). It is supposed that the entoplastron and epiplastron correspond to the interclavicle and clavicle of other forms. In some *Chelonia* the pieces of the plastron are in contact by their whole margin and form a continuous plate (*Testudinidae*, etc.).

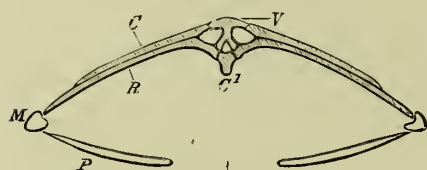


FIG. 225.—Transverse section of the skeleton of *Chelone midas* in the dorsal region (from Huxley). *C*<sup>1</sup> centrum; *V* neural plate; *C* costal plate; *R* rib; *M* marginal plate; *P* lateral element of the plastron.

The shell is covered externally by the horny epidermal shields. These are applied to the outer surface of both the carapace and plastron. They are regularly arranged but by no means correspond with the subjacent bony pieces, on the surface of which they leave sutural markings. There is some variation in their arrangement, but typically there is on the dorsal surface, a median row of five shields (*vertebral*), two lateral rows of four shields (*costal*), and a marginal row of twenty-four or twenty-five shields (*marginals*) of which the anterior median is called *nuchal*, and the posterior *pygal* or *supracaudal*. On the ventral surface are six pairs of shields, called, from before backwards, the *gular*, *humeral*, *pectoral*, *abdominal*, *femoral*, and *anal*. In front of the *gulars*, there is usually a paired or unpaired *intergular*, and ventral to the marginal shields, between them and the shields of the ventral surface there is a variable

number (often five or six) of *inframarginals*. In addition to these scale-like plates, small horny structures are formed on other parts of the body, especially on the limbs and head.

The horny plates are formed as cornifications of the outer parts of the epidermis. They are added to throughout life, increasing both in area and thickness. The annual additions often leave marks in the form of rings.

The vertebrae are few in number. There are usually eight cervical, ten trunk (thoracic), two sacral and a variable number of caudal. The cervical vertebrae are without transverse processes or ribs, and the neural spines are low or absent. They are freely moveable upon one another, and their neurocentral sutures persist.

The trunk or thoracic vertebrae bear ribs and are firmly connected with the carapace by their neural spines and ribs. They are without transverse or articulating processes, and the neural arches are but loosely attached to the centra. The ribs are attached partly to the neural arches and partly to the centra. The sacral vertebrae bear short ribs which are not ankylosed either to them or to the ilia. The caudal vertebrae are procoelous and freely moveable. They bear short ribs which may be fused with the vertebrae and appear as transverse processes.

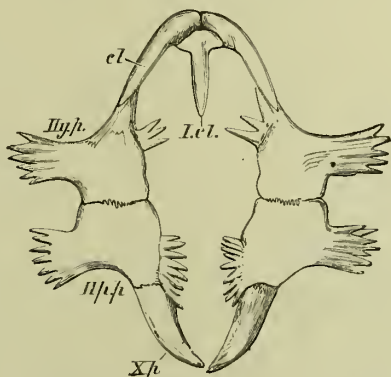


FIG. 226.—The plastron of the green turtle (*Chelone mydas*) (from Huxley). *L.cl* interclavicle; *cl* clavicles; *Hy.p* hypoplastron; *H.p.p* hypoplastron; *X.p* xiphiplastron.

The atlas is composed of three pieces, one ventral and two dorso-lateral. The axis carries the centrum of the atlas as an odontoid process. The character of the articulating surfaces of the centra varies considerably. In *Chelone mydas* the second and third vertebrae are opisthocoelous, the fourth is biconvex, the fifth and sixth are procoelous, the seventh has a flat anterior and a convex posterior surface, the eighth is concave in front and convex behind. The centrum of the eighth is short, its neural spine expanded (attached by ligament to the nuchal plate); its postzygapophyses arch over the prezygapophyses of the first thoracic vertebra. The thoracic vertebrae have flattened faces and are firmly united by cartilage. The

first differs from the others; it is procoelous, it has a pair of prezygapophyses, its spine is not connected to a neural plate, and its rib has no costal plate but is connected with the costal of the next vertebra. The neural arch of this vertebra occupies only the anterior part of its centrum. The neural arch of the second thoracic overlaps the centrum of the first, occupying the anterior half of its own and the posterior half of the preceding centrum. This applies to the next eight thoracic vertebrae, and also to their ribs which are carried forwards with the arch and articulate, not only with their own centrum and arch, but also with the centrum and arch of the preceding vertebra. In the tenth vertebra the neural arch is confined to the anterior part of its own centrum and the ribs, which are short and without costal plates, meet those of the preceding vertebra.

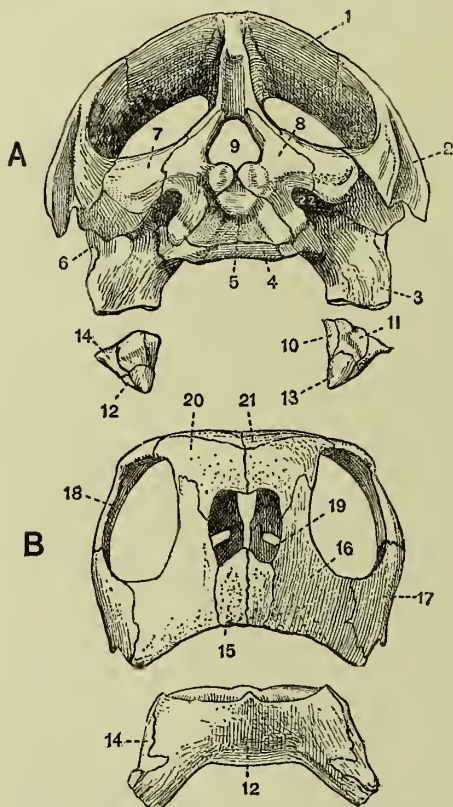


FIG. 227.—A. Posterior, B. Anterior view of the skull of *Chelone midas* (from Reynolds). 1 parietal, 2 squamosal, 3 quadrate, 4 basisphenoid, 5 basioccipital, 6 quadrato-jugal, 7 opisthotic, 8 exoccipital, 9 foramen magnum, 10 splenial, 11 articular, 12 dentary, 13 angular, 14 supra-angular, 15 premaxilla, 16 maxilla, 17 jugal, 18 postfrontal, 19 vomer, 20 prefrontal, 21 frontal, 22 external auditory meatus leading unto tympanic cavity.

The skull (Figs. 227, 228) possesses only one temporal arcade, the lower, and the lateral temporal fossa is therefore absent. In this respect the skull is mammal-like. The roof consists of a supraoccipital with a strongly developed occipital crest, a pair of parietals and a pair of frontals. There is no pineal foramen.

Descending lamellar processes of the parietals (Fig. 228, 1) reach down to the pterygoids and take the place of the alisphenoids, which are absent. Presphenoid and orbitosphenoids are also absent. The epiotic is united to the supraoccipital; the opis-

thotics remain separate, as does the prootic which forms part of the side wall of the cranial cavity. All the parts of the maxillo-palatine apparatus as well as the quadrate are firmly connected with the bones of the skull. The naso-ethmoidal cartilage largely persists, and is covered dorsally by two bones, which assist in forming the anterior margin of the orbit and occupy the position of the nasal, prefrontal and lacrymal (Fig. 227, 20). The palatines usually have palatal plates which join with a ventral expansion of the median vomer to form a hard palate. The premaxillae are small. The maxillae are large and are

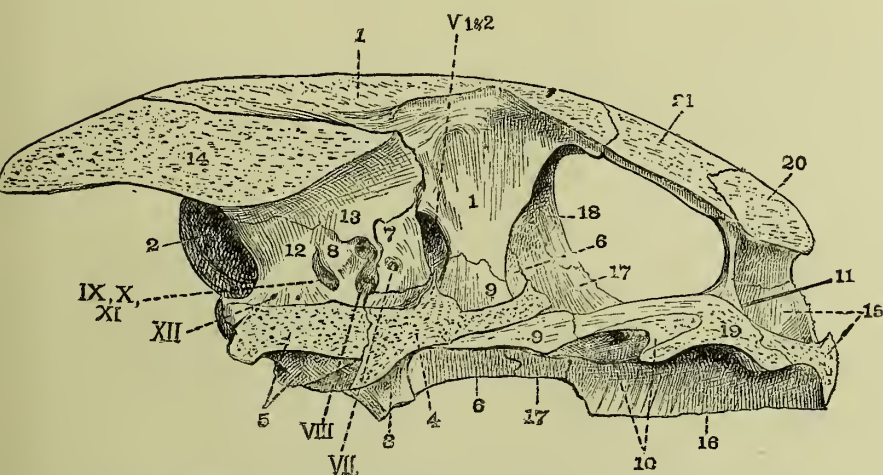


FIG. 228.—Longitudinal vertical section through the cranium of *Chelone midas* (from Reynolds). 1 parietal, 2 squamosal, 3 quadrate, 4 basisphenoid, 5 basioccipital, 6 quadrato-jugal, 7 prootic, 8 opisthotic, 9 pterygoid, 10 palatine, 11 rod passed through the nasal passage; 12 exoccipital, 13 epiotic, 14 supraoccipital, 15 premaxilla, 16 maxilla, 17 jugal, 18 postfrontal, 19 vomer, 20 prefrontal, 21 frontal. V-XII foramina for exits of the corresponding cranial nerves.

followed by the jugals and quadrato-jugals which reach back to the quadrate. The quadrate (Fig. 227, 3) projects downwards from the petiotic and has an articular surface for the mandible. It is overlaid by the squamosal (2). In many *Chelonia*, particularly the marine forms, the temporal fossa is roofed over by bone consisting of a horizontal shelf from the parietals which meets the postfrontals and squamosals (Fig. 227 A). The orbit is completely enclosed by bone, consisting of postfrontal, frontal, prefrontal, maxilla, and jugal. In *Cistudo* and *Geomyda* the quadrato-jugal is absent and the infra-temporal arcade



therefore incomplete. The columella auris is bony and reaches from the fenestra ovalis to a small cartilage in the tympanum. In the mandible, the two dentaries are fused, as in birds, and five pairs of other bones are present (articular, angular,

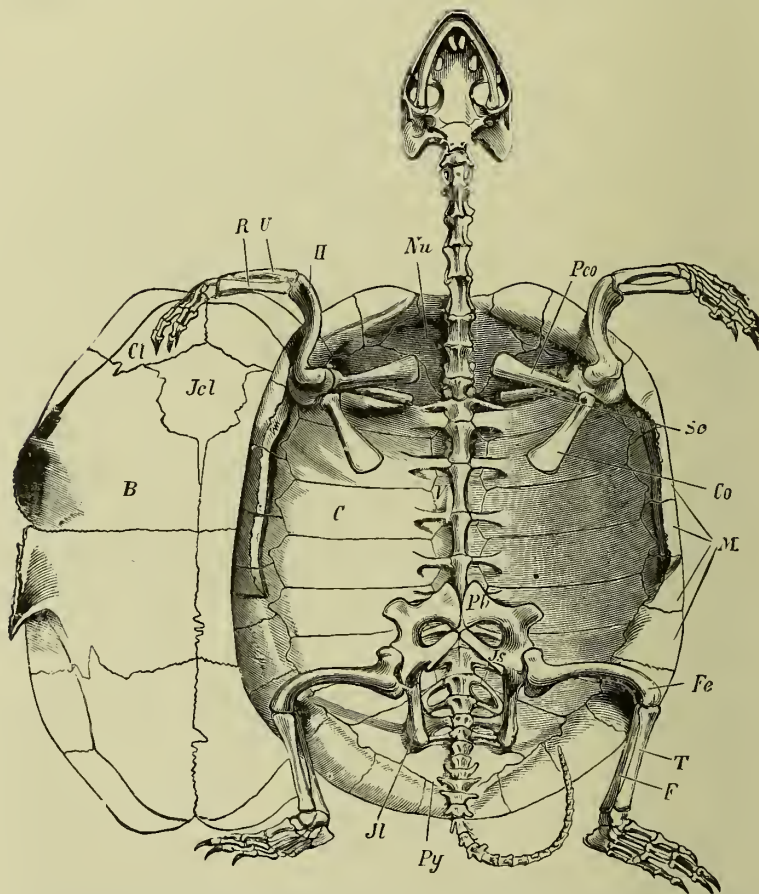


FIG. 229.—Skeleton of *Emys europaea*, in ventral view with plastron turned to one side (from Claus). *B* plastron; *C* costal plates; *Cl* epiplastron (clavicle); *Co* coracoid; *F* fibula; *Fe* femur; *H* humerus; *J cl* entoplastron (interclavicle); *Jl* ilium; *Is* ischium; *M* marginal plates; *Nu* nuchal; *Py* pygal plate; *Pb* pubis; *Pco* precoracoid (acromial process); *R* radius; *Sc* scapula; *T* tibia; *U* ulna; *V* neural plates.

surangular, splenial, and coronoid). The hyoid consists of a cartilaginous basilingual plate and of two pairs of ossified cornua, which have no direct connection with the skull.

Teeth are completely absent, but the jaws, both upper and



lower, are covered by cutting horny plates, like the beak of a bird, which enable some species to bite with great vigour and to inflict considerable wounds.

Both sternum and sternal ribs are absent.

The four limbs enable the *Chelonia* to creep and run on land ; in the aquatic forms, however, they are swimming feet or fins. The position of the pectoral and pelvic girdles between the carapace and plastron is remarkable (Fig. 229), but in the foetus they are placed, respectively, in front of and behind the ribs, and only become covered by the latter as development proceeds. In the pectoral girdle the scapula, the upper end of which is attached by cartilage or ligament to the first costal plate, and precoracoid are ossified continuously and form one bone (*Sc*, *Pco*). The coracoid (*Co*) is distinct. The precoracoids and coracoids do not form a ventral symphysis but are connected by ligament. There is no clavicle, unless the epiplastra can be called such. The fore limb is typical. The manus has five digits and the carpus consists of the typical nine ossicles, but there is sometimes a certain amount of fusion. In the pelvis the ilia unite with the sacral ribs, and in some genera by ankylosis with the last costal plates. There is a pubic and ischiadic symphysis, but the pubes and ischia are separate ventrally (Fig. 229, *Pb*, *IS*). The hind limb has five digits, and the tarsus contains the usual bones, but it is less typical than the carpus and there is generally a certain amount of fusion amongst its elements.

The tongue is attached to the floor of the buccal cavity and is not protrusible. The lungs are highly developed spongy structures attached by their whole length to the inner surface of the shell. They are covered on their ventral surfaces by a muscular diaphragm-like membrane, which is attached to the bodies and ribs of the third and fourth dorsal vertebrae. The respiratory movements of air are caused, partly by the protrusion from and retraction into the shell of the head and limbs, and partly by swallowing movements in which the hyoid apparatus participates. They can usually exist a long time without breathing.

A membranous epiglottis is sometimes present. There are no vocal chords, but some *Chelonia* have a feeble piping voice. In the genus *Cinyx* the trachea and bronchi are curved.

The intestine is without a caecum. The cloaca contains, at-

tached to its ventral wall, a large copulatory organ, and receives the opening of the bladder.

In both sexes the urinary and generative ducts open separately into the neck of the bladder, which must be regarded as a urinogenital sinus.

The penis,\* which is a development of the ventral wall of the cloaca, ends freely in a glans penis, and is marked on its dorsal side by a groove

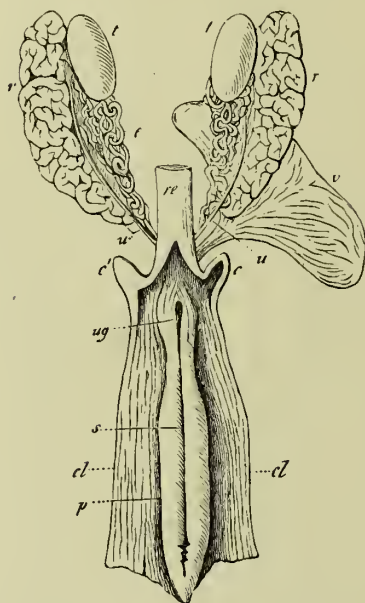


FIG. 230.—Cloaca and urinogenital organs of *Chelydra serpentina* (from Gegenbaur). The cloaca is laid open from the dorsal side. *c, c'* blind sacs of cloaca; *cl* cloaca; *e* epididymis and vas deferens; *p* penis; *r* kidneys; *re* rectum; *s* groove on penis; *t* testis; *u* ureter; *ug* cloacal opening of urinogenital sinus (bladder); *v* bladder.

which contains in its front end the opening of the bladder (Fig. 230). The penis consists of a fibrous body (Fig. 231), which bifurcates in front and is attached, not to the pelvis, but to one of the dorsal vertebrae, and of some erectile tissue (Fig. 231) round the groove and in the glans. In the female there is an organ, the clitoris, similar to the penis but less developed.

**Peritoneal canals**† are present. Their abdominal openings are placed in a recess of the peritoneum close to the neck of the bladder. They lie in the penis near the groove, and either end blindly in the glans or open into the cloaca at the base of the glans. In the female they run in the ventral wall of the cloaca and open near the glans of the clitoris.

The **suprarenal bodies** are two rather long, yellow bodies on the inner surface of the kidneys.

The eyes are contained in closed orbits and possess upper and lower lids and a nictitating membrane.

There is no pecten. Lacrymal and harderian glands are present.

There is always a tympanic cavity with a wide eustachian tube not enclosed in bone, a long columella auris, and a tympanic membrane visible externally.

**Vascular system.** The sinus venosus is distinct and receives

\* Boas, *Morph. Jahrb.*, 17, 1891, p. 271. Gadow, *Phil. Trans.*, 1887, 178, p. 5.

† Gadow, *l.c.*

some of the hepatic veins as well as the three systemic veins. The auricular septum is complete, but the ventricular septum is incomplete. The pulmonary artery and the left aortic arch arise from the right side of the septum, the right aortic arch from the left. The right arch gives off two innominates (Fig. 232); the left arch gives off the coeliac. The pulmonary artery is connected with the systemic on each side by open ductus Botalli. The apex of the ventricle is as in the *Crocodylia* connected with the pericardial wall by a ligament. There are two anterior abdominal veins (p. 326).

The copulation may last a day, and during its process the male is carried on the back of the female. The eggs are laid in small number except in the marine forms in which they are more numerous. They contain within the shell, which is either parchment-like or hard and calcareous, a layer of albumen surrounding the yolk, and are buried in the earth, in the aquatic forms near the shore. According to Agassiz (*l.c.*) the North American marsh tortoises lay eggs only once a year, while they copulate twice (in the spring and autumn). The first copulation, according to this investigator, takes place in *Emys picta*, in the seventh year, the first deposition of eggs in the eleventh year of the animal's life. These facts agree with the slow growth of the body of tortoises and the great age which they attain.

The Chelonians belong mainly to warmer climates, and live principally on vegetables. Many of them, however, also eat mollusca, crustacea, fish, etc. Terrestrial, fresh-water, and marine forms are known, and there are about 260 living species.

The earliest remains of Chelonia are from the Upper Trias (Keuper) and present no approximation to any other form of Reptile. According to the present state of our knowledge they reached their greatest development towards the end of the Mesozoic and in the earlier part of the Tertiary period.

As an interesting indication of the incompleteness of the geological record, and of the inadvisability of concluding that because fossil remains are not found at any particular period,

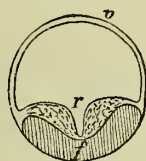


FIG. 231.—  
Transverse  
section through  
the cloaca of  
a Chelonian  
diagrammatic  
(after  
Boas from  
Gegenbaur). *f.*  
fibrous body  
on which the  
penial groove  
*r* surrounded  
by erectile tis-  
sue runs; *v*  
wall of cloaca.

the animals were not then existing, it may be mentioned that the earliest known Chelonians were in every way as specialised as those now living.

**Sub-order 1. ATHECAE.** Vertebrae and ribs free, not fused with the carapace, which consists of numerous juxtaposed polygonal plates. The skin is leathery without horny plates. There are eight plastral elements in the ventral part of the shell. The parietal bones are without descending processes, and nearly cover the supraoccipital; the temporal fossa is roofed in. Neuro-central suture on all the vertebrae except the posterior caudal,

the cervicals are short and the head is not retractile. The limb-girdles are essentially like those of other Chelonians; limbs paddle-shaped, clawless; digits of fore-limb elongate. Marine, within the tropics of the Indian, Atlantic, and Pacific Oceans.

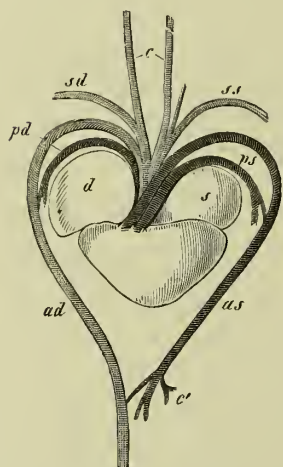


FIG. 232.—Heart and great arteries of a Cheloniann (*Chelydra*), (from Gegenbaur). *d* right, *s* left auricle; *c* carotid; *ad* right, *ps* left aortic arch; *pd* right, *ps* left pulmonary artery; *c'* coeliac artery; *sd* right, *ss* left subclavian artery.

The pedigree of this sub-order has been much disputed. As an indication of the slight value of all such speculations, it may be mentioned that it has by some authorities (Cope, Dollo, Boulenger) been regarded as the most primitive of recent *Chelonia*, by others (Baur, Dames, Case) as the most specialised. *Dermochelys* Blainv. (*Sphargis* Merrem); only one species. *D. coriacea* L. reaches 6½ ft., small specimens (to 3 in.) and large specimens only known—breeds on sandy shores, flesh unwholesome. Fossil forms from the Upper Cretaceous and Ter-

tiaries, *Protostega*. Cope, *Proctosphargis* Capellini, *Psephophorus* H. v. Meyer, *Eosphargis* Lyd.

**Sub-order 2. THECOPHORA.** Thoracic vertebrae and ribs immovably united with a series of median (neural) dermal plates and a paired series of lateral (costal) dermal plates. Parietals prolonged downwards meeting the pterygoids or separated from them by an interposed epipterygoid.

#### Section 1. Cryptodira.

Carapace covered with horny shields; neck bending in a sigmoid curve in a vertical plane; pelvis not fused with the carapace.

Fam. 1. **Chelydridae**. Nuchal plate with long costiform processes underlying the marginals; plastral bones nine; tail long; snout with powerful hooked beak; temporal region incompletely roofed over; fingers and toes webbed, with claws; very fierce. *Chelydra* Schweigg. N. Amer. to Ecuador, the snapping turtle, edible. *Macrochelymys* Gray, alligator-turtle, N. Amer. Both genera may leave the water. *Platycheilus* A. Wag. Upper Jur.

Fam. 2. **Dermatemydidae**. Nuchal plate with costiform processes underlying the marginals; plastral bones 9; temporal fossa not roofed over; aquatic, shell to one foot; Central Amer. *Dermatemys* Gray, *Staurotypus* Wagl., *Claudius* Cope.

Fam. 3. **Cinosternidae**. Nuchal plate as above, 8 plastral bones, temporal region not roofed; America n. of Equator. *Cinosternum* Spix.

Fam. 4. **Platysternidae**. Nuchal plate without costiform processes; plastral bones 9, temporal region roofed over; Burma, Siam, S. China, aquatic. *Platysternum* Gray.

Fam. 5. **Testudinidae**. Nuchal plate without well-developed costiform processes, 9 plastral bones, lateral temporal arch usually present, no parieto-squamosal arch; cosmopolitan except Australia and Papuasia; includes terrestrial and aquatic tortoises; about 20 genera. *Kachuga* Gray, India and Burma; *Callagur* Gray, Malay P., Borneo. *Batagur* Gray, Bengal, Burma, Malay P.; *Hardella* Gray, N. India; *Morenia* Gray, N. India and Burma; *Chrysemys* Gray, terrapins or water tortoises, America from Canada to Argentina, carapace flat, feet webbed, tail short; lively and shy; larger species are eaten. *Ocadia* Gray, China; *Malacoclemmys* Gray, N. Amer.; *M. terrapin* extensively eaten in the U.S., and bred in terrapin farms. *Damonis* Gray, E. Indies, China, Japan; *Bellia* Gray, Siam, Burma, Malay P. and Arch.; *Clemmys* Wagl., N.W. Afr., S. Eur., S.W. Asia, China, Japan, N. Amer., aquatic. *Emys* Dum., Eur., N.W. Afr., W. Asia, E. N. Amer.; *E. orbicularis* L. the European pond tortoise. *Cistudo* Flem., N. Amer., a terrestrial tortoise but allied by its structure to the water tortoises; *C. carolina* L., box-tortoise. *Nicoria* Gray, E. Indies, C. and S. Amer. *Cyclemys* Bell, E. Indies, S. China. *Geoemyda* Gray, Burma, Malay P. and Arch. *Chaibassia* Theobald, N.E. India. *Cinixys* Bell, trop. Afr., posterior portion of carapace moveable. *Pyxis* Bell, front lobe of plastron moveable, Madagascar. *Homopus* D. and B., S. and W. Afr. *Testudo* L., plastron immoveable (except in *T. ibera*), since Oligocene, herbivorous and frugivorous, occasionally taking worms, molluscs and insects; eggs hard shelled; usually hibernate in ground or aestivate, nearly 40 species, S. Eur., S. Asia, Africa, S. North Amer., S. Amer.; *T. graeca* the common Greek tortoise; *T. polyphemus* the gopher tortoise of N. Amer. Some tortoises attain a large size, shell to 55 in. (Günther, *Proc. Lin. Soc.*, 1898) in some oceanic islands, e.g. the Galapagos Islands. Mascarenes, Aldabra, Seychelles, etc., where they have recently been largely exterminated; they may attain to a great age, 150 years or more; at the present time indigenous land tortoises are known only on the S. island of Aldabra, representatives of other species only lingering as introduced pets on tropical islands and in Europe.

Fam. 5. **Chelonidae**. Turtles. Nuchal plates without costiform processes; plastral bones nine; temporal fossa completely roofed over; limbs paddle shaped, claws one or two; marine, depositing their eggs in the sand of unfrequented shores, cosmopolitan within the warmer zones. *Chelone* Brong. *Ch. midas* L. the green edible turtle, Atl., Ind., and Pac.



oceans, shell to 4 ft., herbivorous, the dense subcutaneous connective tissue (callipash and callipee) within the shell, as well as the fat and meat, is used in preparing the soup; eggs round, parchment-shelled; *Ch. imbricata*, the hawksbill turtle, shell to 34 in., their horny epidermal shields are used as tortoise shell; *Thalassochelys* Fitzing., *Th. caretta* L. (Fig. 233), the loggerhead turtle, trop. and sub trop. seas.

Two extinct families are allied here:—

The **Chelonemydidae** and the **Thalassemydidae** from the Jurassic, Cretaceous etc.

## Section 2. Pleurodira.

Neck bending laterally; pelvis fused to the shell, the ilia to the carapace, the pubes and ischia to the plastron. Freshwater tortoises almost entirely carnivorous, inhabiting S. America, Australia, Africa, and Madagascar; fossil forms from the Jurassic. The temporal region of the skull

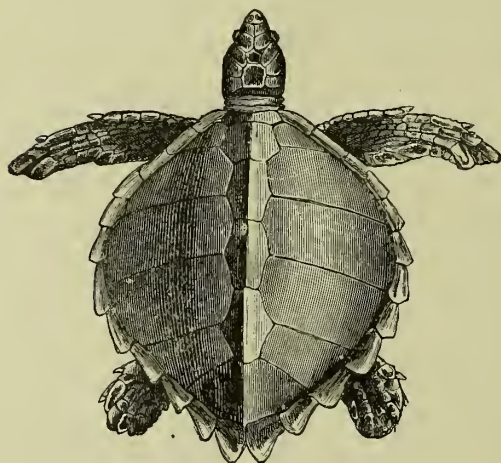


FIG. 233.—*Thalassochelys caretta* (Règne animal).

is variable. The carapace is covered with horny shields except in *Carettochelys*. Extinct forms are known from Trias and Jura of Europe, and are the oldest fossil Chelonia. (*Psammochelys* Quenst. = *Proganochelys* Baur, Keuper Sandstone.)

Fam. 1. **Pelomedusidae**. Neck completely retractile within the shell; carapace without a nuchal shield; plastral bones 11; 2nd cervical vertebra biconvex. Africa, Madagascar, S. America. *Sternotherus* Bell, skull without

supratemporal roof, quadrato-jugal widely separated from parietal, digits short, 5 claws, trop. and S. Afr., Madagascar; *Pelomedusa*, Wagl., skull with a slender parieto-squamosal arch, digits short, 5 claws, Africa and Madagascar; *Podocnemis* Wagl., supratemporal roof formed by junction of parietal with quadrato-jugal, digits webbed, 5 claws on fore- and 4 on hind-foot, S. Amer., Madagascar; *P. expansa*, Arran turtle, edible, eggs collected for oil, S. Amer.

Fam. 2. **Chelydidae**. Plastral bones 9, temporal region diverse, S. Amer., Australia, New Guinea. *Chelys* Dünér., digits webbed, S. Amer. and Australia, *Ch. fimbriata* Schn., the matamata, aquatic. *Hydro-medusa* Fitz., digits webbed, long neck, S. Amer. *Chelodina* Fitz., long neck, neural plates absent, costals meeting, digits webbed, Australia and New Guinea. *Rhinemys* Wagl., S. Amer.; *Hydraspis* Bell, S. Amer.; *Platemys* Wagl., S. Amer.; *Emydura* Bon., Australia and New Guinea; *Elseya* Gray, Australia.

Fam. 3. **Carettochelydae.** Horny shields absent, shell covered with soft skin, limbs paddle-shaped, neck not retractile; *Carettochelys* New Guinea.

Section 3. **Trionychoidea.** Mud tortoises.

Shell flat oval and almost round, covered with soft leathery skin, without horny shields, digits broadly webbed, the 3 inner digits only with claws, articulation between the last cervical and first dorsal by zygapophyses only, pelvis not anchylosed to shell; 4th digit with 4 or more phalanges; marginals absent or incomplete, not joined to ribs. Head and neck retractile, bending in vertical plane, nose as a short soft proboscis, temporal fossa not roofed; first in the Upper Cretaceous; carnivorous, rivers of Asia, Africa and N. America, in the muddy bottom of shallow waters. *Trionyx* Geoffr., Africa, Asia, N. Amer., *T. ferox* Schn., soft-shelled turtle, U. S.A., voracious, active, edible, flesh surpassing that of the green turtle. *Pelochelys* Gray, E. Indies; *Chitra* Gray, E. Indies; *Cycloderma* Ptrs., trop. Afr.; *Emyda* Gray, E. Indies; *Cyclanorbis* Gray, trop. Afr.

## CHAPTER XII.

### AVES.\*

*Warm-blooded oviparous bipedal animals, covered with feathers. The chambers of the heart are completely separated. The right aortic arch alone persists. There is a single occipital condyle, and the anterior limbs have the form of wings.*

Birds are warm-blooded animals possessing a temperature, which is generally higher than that of Mammals, reaching in some cases, it is said, 112° F. and is maintained pretty constantly irrespective of that of the surrounding air. This condition demands on the one hand a great energy of metabolism and on the other a regulating mechanism by which the loss of heat is controlled. The metabolism is undoubtedly favoured by the respiratory arrangements, which ensure, in birds, a very complete oxidation of the blood. Not only do the lungs by their complexity of structure expose a very large absorptive surface, but the curious extensions of the bronchi into thin-walled air-sacs, which extend among the viscera and into the bones, no doubt assist in the oxidation processes by acting as reservoirs

\* C. L. Nitzsch. *System der Pterylographie*, Halle, 1840. Gray & Mitchell, *The Genera of Birds*, London, 1841-9. C. E. Sundevall, *Tentamen*, Stockholm, 1872-3: English Edition, London, 1889. T. Huxley, On the classification of Birds, *Proc. Zool. Soc.*, 1867. Stejneger, Birds in vol. 4 of the *Standard Natural History*, Boston, U.S.A. 1885. M. Fürbringer, *Untersuchungen zur Morphologie u. Systematik der Vögel*, Th. 1 and 2, 1888. H. Gadow, Aves, *Bronn's Thierreich*, 1 and 2, 1891, 1893. A. Newton, *Dictionary of Birds*, London, 1893-6. A. H. Evans, Birds, in the *Cambridge Natural History*, 1899. W. P. Pyecraft, Morphology and Phylogeny of the Palaeognathae (Ratitae and Crypturi) and Neognathae (Cariinatae), *Trans. Zool. Soc.*, 15, 1900, p. 149. W. K. Parker, an important series of memoirs on the anatomy and development of various birds, a list of which will be found in the above-cited *Dictionary of Birds*, Introduction, p. 80, note 2.

which supply unvitiated air to the pulmonary passages during the expiratory act (see below). The regulating mechanism cannot be properly treated here, indeed it is not fully understood, but the protection against loss of heat by radiation from the external surface by the feathers is one obvious factor and the loss by evaporation from the internal surface of the air-sacs must be another, birds being without the cutaneous sweat-glands which are so characteristic of mammals. Though during prolonged frost and snow numbers of birds perish, it is rather from the want of food than the inability to bear cold, and the habit of migration, which among birds is carried to such an extreme, is undoubtedly prompted rather by the desire to obtain food than to avoid cold. This is obvious from the fact that in the most northern regions the migratory movement southward begins before the full summer warmth is there felt. This movement dispenses with the necessity of passing into a torpid condition which is so common among many of the mammals that winter in northern countries, and some of the land-birds which remain to brave a temperature that might otherwise endanger life are endowed with additional feather-clothing (*Lagopus*, *Linota*, some owls, etc.).

The most essential peculiarity of birds is their power of flight. Their whole organisation, both internal and external, is modified in correlation with this peculiarity. In this connection we may call attention to the great uniformity of structure presented by the class, and the sharp definition of its characters. Between the extremes of avine organisation there is less difference than in a single order of mammals, and there are no forms transitional between birds and other classes of vertebrata. It is true that they are not the only vertebrates which have achieved the aerial habit. The pterodactyls amongst reptiles and the bats amongst mammals have also developed the power of flight. But in these animals the power depends upon quite other modifications than in birds, and although it is incontestable that reptiles are the nearest allies of birds, there is no single family of reptiles from which they can be derived, least of all from the pterodactyls. Moreover these groups are comparatively small and unimportant, whereas birds are a dominant group at the present time and exceed all other vertebrate classes in number of species though not in variety of organisation. The origin of birds is a

much-vexed question. As stated above they are reptilian in their affinities, but there are no transitional forms connecting them with reptiles. They make their appearance in the Upper Jurassic, and the earliest bird known—*Archaeopteryx*—presents almost all the features of specialisation characteristic of living forms. Whatever may have been the origin—whether from reptilian or from proreptilian creatures—of their peculiar type of structure, the avine is the only vertebrate organisation which has enabled its possessors to make a complete conquest of the air and to fill it with a countless number of inhabitants. But although a new world has been opened to them, their organisation, except in trivial details, has not responded to the infinite diversity of the new environment. This is a fact not without significance to the student of organic evolution, and one to which we shall return when considering that subject in its wider aspects. Meanwhile we may note that the achievement of the power of flight by an animal of the bulk of a bird has been a rare phenomenon in nature; so rare indeed that birds are practically without competitors in their aerial surroundings. This may account for the small amount of structural modification met with in the class, but on the other hand it suggests that the adjustments of machinery necessary to enable an animal of the weight of a fair-sized bird to fly with ease and certainty are so delicate and minute that no departure from them is possible, a suggestion which receives some corroboration from the consideration that the most remarkable of the not very remarkable deviations from the normal avine type are presented by birds which have lost the power of flight and have become adapted exclusively to a terrestrial or aquatic life; we refer to the Ratitae and the penguins. It is interesting to note that rising from the ground or water appears to have been one of the greatest difficulties which nature has had to overcome in enabling birds to fly. Some of the strongest and most enduring flyers experience a difficulty in this respect, e.g. the albatrosses. A further point to be noticed is that the power of flight appears to be inconsistent with great size and weight. The largest flying birds, e.g. the vulture, bustard, swan, turkey, etc., are not large or heavy animals, and in no case in which considerable size and weight has been attained is the power of flight present.

The flight of birds is entirely effected by the anterior extre-



mities, their movements on land by the posterior. They are bipedal and their legs are attached comparatively far forward. In correspondence with this the union between the pelvis and the vertebral column is both extensive and strong. Posteriorly the body is prolonged into a short caudal stump (*uropygium*), the last vertebrae of which serve for the support of a group of stiff steering or tail feathers (*rectrices*). In front it is prolonged into a flexible neck, on which is balanced a light rounded head with a projecting beak. The anterior appendages, which are transformed into wings, lie folded at the sides of the body.

Arrangements for lessening the weight of the body are discernible, especially in the structure of the osseous skeleton. The bones contain air-spaces (*pneumaticity*), which communicate with the air-sacs of the lungs through openings in the osseous substance, which is in such cases confined to a relatively thin layer. Pneumaticity is most developed in those birds which combine a quick and enduring power of flight with a considerable size of body (albatross, pelican, etc.), and is, speaking generally, least developed in small birds and in aquatic birds. It is almost absent in passerine birds, swifts, divers, rails and the *Apteryx*, and is not found in young birds. When air-spaces are not present the larger bones contain marrow.

Teeth are not present at any stage of their existence in living birds. Their place is taken by the horny coverings (*rhampotheca*) which ensheath the upper and lower jaws. The external nostrils are placed on the upper surface near the root of the upper beak, except in *Apteryx* where they are terminal. The *cere* is the soft skin which covers the base of the upper beak. The *lore* is the space between the beak and the eye. The eyes are usually remarkably large; they possess upper and lower lids, and a well developed nictitating membrane which can be drawn across the eye from its inner (anterior) angle. The external auditory meatus is short and its opening is often surrounded by a circle of larger feathers (auriculars), and in a few birds (e.g. some owls) is overlapped by a cutaneous valve which is likewise beset with feathers and constitutes a kind of pinna. A proper pinna is never present.

The anus (*vent*) is at the hind end of the body at the root of the tail. On the dorsal side of this part of the body is placed the opening of the uropygial or oil-gland, a cutaneous gland the secretion of which the bird uses when preening its feathers.

The most important feature in the external appearance of birds is their covering of feathers. The skin is naked in a few places only—as on the beak, the cere, the toes, (with a few exceptions, *Lagopus*, etc.), usually on the tarsometatarsus, sometimes on the neck (vulture), or even on the abdomen (ostrich), and on the cutaneous outgrowths of the head and neck (gallinaceous birds, vulture). While the cere is soft, the edges of the rhamphotheca are usually cornified, and are only exceptionally soft (ducks, snipe), and are then richly innervated, serving as a fine tactile organ. The skin on the toes and metatarsus is cornified so as to form a firm horny covering, which is sometimes granular, more often divided into scales, and which may afford important systematic characters. When this integument is scaly in front and smooth behind, the metatarsus is said to be *laminiplantar* (thrushes and other Oscines). The following special horny structures may be mentioned : the claws on the toes (and sometimes on the first and second digit of the manus), the spurs on the posterior and internal edge of the metatarsus in the male Gallinaceae, and on the carpus (some Charadriidae, etc.).

Feathers are closely allied to scales. On the wings of penguins the small feathers present are hardly distinguishable from scales. They arise by the cornification of the epidermis of papillae containing a vascular core. These papillae at first project freely on the surface, therein differing from hairs, but they very soon become secondarily enveloped in a pit (follicle) which gradually deepens as the development continues.

A typical feather consists of the following parts : There is a stiff axial rod, the *scapus* or *stem*, running the whole length of the feather. This consists of two parts ; the proximal, hollow, semitransparent *calamus* or *quill*, and a distal part, the *shaft* or *rhachis*. The calamus is cylindrical, is partly embedded in the skin, and encloses the dried up vascular papilla of the growing feather ; at its proximal end is a small opening, the *inferior umbilicus*, and at its distal end where it passes into the rhachis there is on the ventral side, i.e. on the side adjacent to the body, a second opening, the *superior umbilicus*. The rhachis is solid, somewhat quadrangular, and grooved on its ventral surface ; it carries a number of lateral processes, the *barbs* (*rami*), which again carry still smaller processes the *barbules* (*radii*). The barbs and barbules constitute the *vane* (*rexillum*) or web of the

feather. The barbs are narrow elastic laminae which project obliquely on each side from the rhachis. The barbules are also set obliquely on each side of the barb, in such a way that those on the distal side of a barb, i.e. those pointing towards the apex of the feather, cross several of the barbules on the proximal side of the next barb, i.e. on the side of the barb turned towards the quill end of the feather. The distal barbules possess on their lower face, i.e. on the face turned towards the body of the animal, a number of minute processes (*barbicels* or *cilia*) with hooked terminations (*hamuli*). The upper edges of the proximal barbules are folded over so as to form a flange with which the hamuli of the distal barbules of the adjacent barbs interlock. In this way the barbs on each side of the rhachis are closely connected together into an almost air-tight web. The *hyporhachis* or *aftershaft* is a second shaft arising from the calamus just proximally to the superior umbilicus. In the cassowary it is as large as the main shaft, but in other birds it is much smaller, and is sometimes absent. It possesses barbs and barbules, but not barbicels. In the developing feather the vascular pulp of the quill extends through the superior umbilicus along the ventral side of the rhachis. The two rows of barbs converge at the proximal end of the rhachis so as to run into one another proximally to the superior umbilicus.

According to the nature of the rhachis and barbs, the following kinds of feathers may be distinguished: *Contour feathers* (*pennae*) with stiff shaft and firm vexillum; *down feathers* (*plumulae*) with soft shaft and vane, and without hooks; *filoplumes* with slender hair-like shaft with few or no barbs. The contour feathers appear on the surface and attain their greatest development as the *remiges* (wing-quills) in the wing and the *rectrices* (tail-quills) in the tail; they usually possess hamuli. The down feathers form the deep layer of the plumage and are covered by the contour feathers; they serve for the retention of warmth, and in some cases are without a shaft, the barbs arising in a tuft from the end of the quill. The filoplumes are distributed among the contour feathers and arise near their base. There are many forms of feather intermediate between these principal forms. *Powder-downs* are down feathers the ends of which break off into a fine dust; they occur in patches

(herons, some parrots, etc.). *Nestling downs* (*neossoptiles*) are down feathers with certain characters of their own found on the newly-hatched bird. In the autumn there is usually a complete change of feathers (*autumnal moult*), whereas in the *spring moult*, by which the bird acquires its breeding plumage, there is only rarely a complete new formation of the plumage. As a rule, the spring moult is accompanied by a change of colour of the feathers (probably due to chemical change in the pigment already

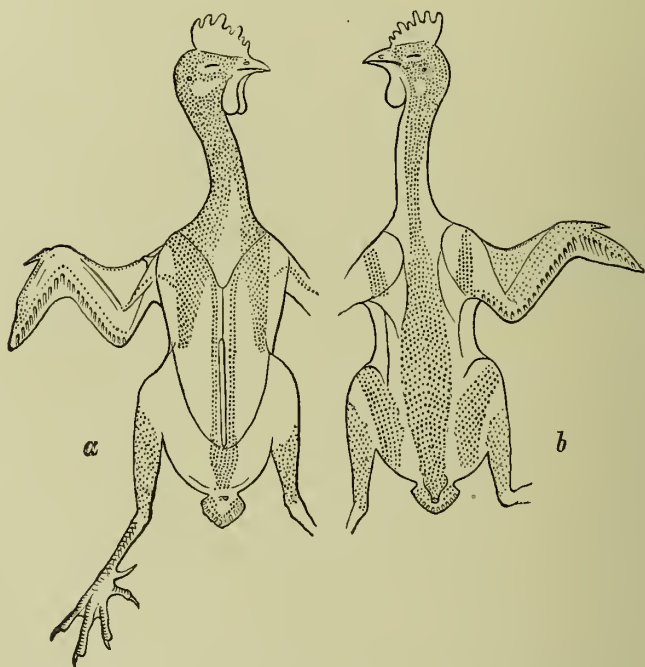


FIG. 234.—Pterylae and apteria of *Gallus bankiva* (after Nitzsch) *a* ventral, *b* dorsal.

present), and sometimes by a mechanical breaking off of certain parts of the feathers. The new feathers of the moult are formed in the follicles and from the pulp of the old feathers.

The plumage is only rarely distributed evenly over the whole of the body (Ratitae, penguins). Usually the contour feathers are arranged in rows—the *pterylae*, between which there are spaces—the *apteria*, which are naked or only covered with down (Fig. 234). The form and distribution of these feather tracts present modifications which can be used in classification.

The grouping of the feathers on the anterior limb and on the tail determines the utility of these organs as wings and steering apparatus respectively. The wing can be folded at two points, viz., at the elbow joint and the carpal joint; its surface is formed by the large remiges attached to the forearm and manus, and partly by special folds of skin which stretch between the body and the posterior side of the proximal part of the humerus (*post-patagium*), and between the upper-arm and fore-arm on the pre-axial side (*prepatagium*, Fig. 234). The prepatagium contains an elastic band which extends along its outer edge from the humerus to the wrist, and which, when the fore-arm is extended, exercises a traction on the thumb side of the carpal joint, and so causes the simultaneous extension of the hand.

The large wing quills (*remiges*) are attached along the post-axial border of the fore-arm and manus to the bones of these parts. Those which are attached to the manus are larger than the others and are called *primaries* or *manuals* (Fig. 235 *HS*); while

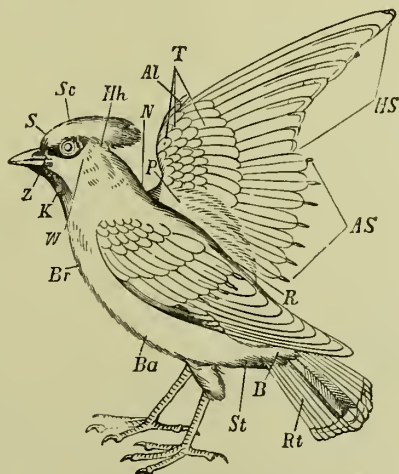


FIG. 235.—Nomenclature of the plumage and body-regions of *Ampelis garrulus* (wax-wing). Slightly modified (after Reichenbach). *AL* bastard wing; *AS* secondaries; *B* tail-coverts; *Ba* belly; *Br* breast; *Hh* hind head; *HS* primaries; *K* throat; *N* nape; *P* scapulars; *R* back; *Rt* tail with tail-quills; *S* forehead; *Sc* occiput; *St* vent; *T* coverts; *W* cheek; *Z* lore.

those which are attached to the fore-arm are called *secondaries* or *cubitals* (Fig. 235 *AS*). There are usually ten primaries; of these some are attached to the metacarpals (metacarpal quills), the others to the phalanges of digits 2 and 3 (digitals); none are attached to the pollex. The secondaries vary in number (six to thirty or more); they are attached to the ulna. It happens in some birds (*Anseres*, *Colymbidae*, *Psittaci*, *Accipitres*, *Columbidae*, etc.) that the fifth cubital (counting from the wrist) is absent, there being a gap between the fourth and sixth (aquinto-cubitalism). The variability of this character extends through



the whole class and is found even in members of the same family.

Covering the bases of the remiges and filling up the gaps between them are smaller pennae called *wing-coverts* (*tectrices*). A small number of pennae attached to the humerus are called *scapulars* (*parapterum*), and some feathers attached to the thumb constitute the *bastard wing* (*alula*). In some birds the wings become so much reduced that the power of flight is almost or quite, as in *Ratitae*, penguins, etc., lost.

The great tail-quills are called *rectrices* (*Rt*), because during flight they are used for steering. There are, as a rule, twelve (sometimes ten or twenty and more) rectrices attached to the last caudal vertebrae in such a way that they can be moved singly, and unfolded laterally like a fan, as well as be all raised or depressed together. The roots of the rectrices are covered by a number of coverts, which in some cases attain an extraordinary size and shape and constitute an ornament to the bird (peacock). When the power of flight is absent the tail loses its significance as a steering apparatus and the rectrices are reduced or absent. In such cases, however, some of the coverts may attain a considerable development as ornamental feathers.

Birds have no sebaceous or sweat glands, but as mentioned above there is an oil-gland on the rump.

The hind limbs, which are principally used in movement upon firm ground, present much diversity, according to the mode of locomotion of the bird. In the first place walking feet (*pedes gradarii*) and wading feet (*pedes vadantes*) are to be distinguished (Fig. 236). In the former the legs are much more completely feathered, being covered at least as far as the tarsal articulation; but they vary considerably. As a rule four toes are present (digit No. 5 being absent), and the first toe is directed backwards, but the following varieties may be distinguished (Fig. 236): All four toes are directed forwards (*p. adhamantes*), e.g. *Cypselus* (*a*), sometimes the inner toe can be turned forwards and backwards (*Colius*); two toes directed forwards and two (1 and 4) backwards (*p. scansorii*), *Picus* (*b*), sometimes the outer toes of this type of foot can be turned both forwards and backwards (*Cuculus*); three toes directed forwards and one back, the anterior toes being free to their roots (*p. fissi*), *Turdus* (*d*); three toes directed forwards, the inner toe backwards, the middle and outer toes united at their roots (*p. ambulatorii*),

*Phasianus* (c); the inner toe is placed behind, the three anteriorly directed toes are fused as far as the middle (p. gressorii), *Alcedo* (e); inner toe behind, the three anterior toes are united by a short membrane (p. insidentes), *Falco* (f). The wading legs

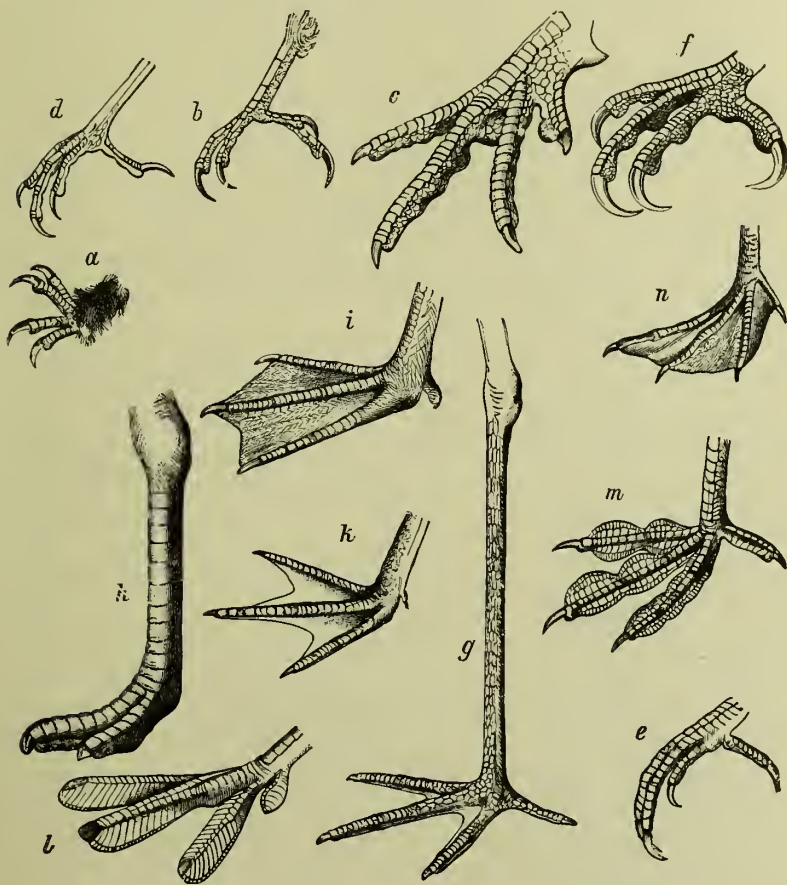


FIG. 236.—The most important forms of birds' feet (b, c, d, f, n, from the *Règne animal*). a *Cypselus apus*; b *Picus capensis*; c *Phasianus colchicus*; d *Turdus torquatus*; e *Alcedo hispidus*; f *Falco biarmicus*; g *Mycteria senegalensis*; h *Struthio camelus*; i *Mergus merganser*; k *Recurvirostra avocetta*; l *Podiceps cristatus*; m *Fulica atra*; n *Phaethon aethereus*.

(p. *vadantes*) as opposed to the walking legs are characterised by the partly or completely unfeathered tibial region; they are found principally in aquatic birds, some of which have a very long metatarsus. The feet of birds with long wading legs may be distinguished into those in which the anterior toes are

united at their roots by a short membrane, *Ciconia* (*g*); and those in which this membranous connection is confined to the middle and outer toes. The short wading legs of the swimming birds, as well as those with long wading legs present with regard to the structure of their feet the following types: Swimming feet, in which the three anteriorly directed toes are connected as far as their extremities by an undivided swimming membrane or web, *Anas* (*i*); half-swimming feet when the web only reaches to the middle of the toes, *Recurvirostra* (*k*); split swimming feet when the toes have an entire cutaneous border, *Podicipes* (*l*); lobed feet when the border is lobed at each joint, *Fulica* (*m*); sometimes the hind toe is included in the web-membrane, *Phaethon* (*n*); finally the hind toe may be completely absent in some wading birds. In the *Ratitae* the inner toe is always absent, and in the ostrich the second digit as well.

Colour is highly developed in the feathers of birds and in some cases in the skin of the head and neck (combs, wattles). It is due either to pigments (absorption colours), or to the structure of the parts acting upon the light after the fashion of a prism or of thin plates (metallic lustre, iridescent colours). Sometimes these two causes combine and produce wonderful effects as in the humming birds, peacock, etc. The blacks, browns, reds, yellows and rarely greens may be due to pigment; blues and violets are due to pigment and structure, there being no blue pigment in birds. In the Touracos (*Musophagidae*) there is a red pigment called *turacin*, which is soluble in water and washes out of the feathers, colouring the water when the animal gets wet or bathes; the birds regain the colour when dry. It is stated that the colour of fully grown feathers, in which the pulp is dry, can in some cases change.

The brain-case (Fig. 237) is arched and spacious, and, except in the *Ratitae* and one or two other groups, the bones become early fused together and the sutures obliterated. The orbits are, except in *Apteryx*, very large. There is a well-marked inter-orbital septum and the facial part of the skull is prolonged into a beak consisting mainly of the premaxillary bones. The infra-temporal arcade is complete, the rod-like jugal (*J*) and quadrato-jugal (*Q j*) reaching back to the quadrate (*Q*). The supra-temporal arcade is usually incomplete, but in some birds, e.g. the fowl, the squamosal sends forward a process which joins the

postorbital process of the frontal. There are no prefrontals, postfrontals, or postorbitals, and the orbit is not closed posteriorly from the temporal fossa, though in parrots the postorbital process of the frontal meets a backwardly directed process of the lacrymal beneath the orbit.

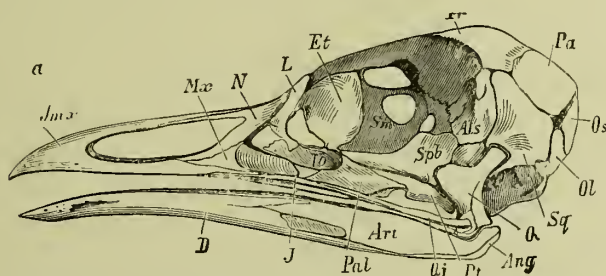
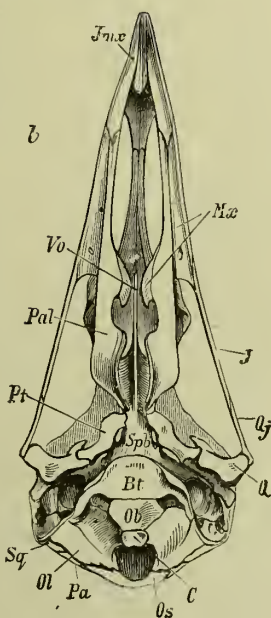


FIG. 237. Skull of *Otis tarda* (bustard). *a* from the side; *b* from below (from Claus). *Als* alisphenoid; *Art* articular; *Bt* basitemporal (parasphenoid); *C* occipital condyle; *D* dentary; *Et* median ethmoid; *Fr* frontal; *J* jugal; *Jmx* premaxilla; *L* lacrymal; *Mx* maxilla; *N* nasal; *Ob* basioccipital; *Ol* exoccipital; *Os* supra-occipital; *Pa* parietal; *Pal* palatine; *Pt* pterygoid; *Q* quadrate; *Qj* quadrato-jugal; *Sm* interorbital septum; *Spb* basisphenoid; *Sq* squamosal; *Vo* vomer.

The squamosal (*Sq*) is closely applied to the skull and is ankylosed with the periotic bones (pro-, epi-, and opisthotic); it often sends a process downwards over the quadrate bone. There are no parotic processes. The quadrate is moveably articulated with the squamosal, the prootic and the alisphenoid. The palate is very imperfect, the posterior nares are between the palatines and the vomer which is usually much reduced, and the maxillaries usually have a maxillo-palatine process (*Mx*). There is no secondary hard palate. The occipital condyle is single and there is no parietal foramen. Parasphenoidal elements are present in the form of the basitemporals which are fused with the base of the skull and as the basisphenoidal rostrum. The *custachian tubes* are included in the basisphenoid and the aper-





tures are near together on the base of the skull. The lower jaw contains, as in other Sauropsida, six osseous elements, viz., articular, angular, surangular, coronoid, dentary and splenial. The *hyoid bone* is prolonged into a posterior rod and consists of three basal pieces, of which the anterior is called the entoglossal bone (Fig. 238, *Ent*), the middle the basihyal (*Co*) and the posterior rod the urohyal. It carries one pair of cornua (*Zh*), which are the homologues of the first branchial arches; these are usually two-jointed and not connected with the skull, but in most woodpeckers they are much elongated and arch over the skull as far as the forehead, constituting in connection with the

muscles of their sheath a mechanism for the protrusion of the tongue. The *columella auris* consists of an osseous rod, the inner end of which fits into the fenestra ovalis while the outer end expands into a triradiate cartilage which is attached to the tympanic membrane.

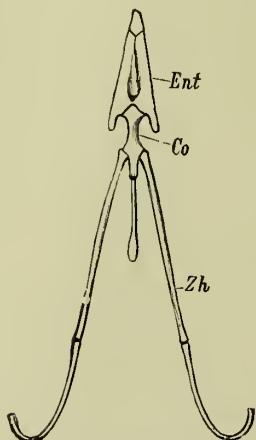


FIG. 238.—Hyoid bone of *Corvus cornix* (from Claus). *Co* basihyal; *Zh* cornua; *Ent* entoglossal bone.

The above are the main features in the avine skull. The following additional points may be noted. The foramen magnum looks downwards as well as backwards. All the occipital bones enter into the foramen magnum, but the condyle is formed almost entirely by the basioccipital. The epiotic and opisthotic fuse with the occipital bones before they unite with the prootic. Basisphenoids and alisphenoids are well developed, but the presphenoid and orbitosphenoids, which enter into the interorbital septum are often imperfect. The interorbital septum (to a varying extent cartilaginous) is formed anteriorly by the mesethmoid (*Et*), which is continuous in front with the (mainly) cartilaginous internasal septum,\* and may appear on the surface of the skull between the nasals and frontals. It is overlaid by the basisphenoidal rostrum. The turbinals or lateral ethmoids are poorly developed. The lacrymals (*L*) are large and perforated by the lacrymal canal. The nasals (*N*) are well developed and form the upper and lateral boundaries of the external nares.† The

\* When the internasal septum is complete the nostrils are said to be impervious (*nares imperviae*), when it is incomplete they are described as pervious (*n. perviae*).

† The term *holorhinal* is applied to those cases in which the external narial opening is oval, the posterior border being curved and in front of the posterior end of the premaxillae. In the so-called *schizorhinal* arrangement the openings are elongated, the posterior border being angular or slitlike and behind the posterior ends of the premaxillae.



premaxillae (*Jmx*) are united into a large triradiate bone. The upper beak is in some birds slightly moveable upon the skull at the posterior ends of the nasals and premaxillae, and in the parrots there is a joint at this point in virtue of which the upper beak has considerable mobility.

There are two vomers but they early unite into a single bone, which is sometimes extremely small or even absent. They underlie the median ethmoid and, except in the ostrich, unite posteriorly with the palatines. The maxillae, which are slender, possess maxillo-palatine plates which may or may not unite with the vomer or with each other ventral to the vomer. The palatines (*Pal*) are elongated bones extending from the premaxillae backwards to the pterygoids, passing ventral to the maxillo-palatines; their hind ends usually join the basisphenoidal rostrum (*Spb*) by an articular surface which allows of their movement on the rostrum. The pterygoids (*Pt*) in front articulate with the palatines and usually with the basisphenoidal rostrum; in some birds there is an additional articulation with the rostrum by means of the basipterygoid processes of the latter (*Ratitae*, some *Carinatae*). Posteriorly the pterygoids articulate with a process of the quadrate. In struthious birds the pterygoids articulate in front with the vomer (except in the ostrich). This also happens in the embryos of many birds, in which the pterygoid extends forwards to the vomer dorsally to the palatine. This forward process in later growth loses its connection with the pterygoid, appearing to segment off from it; it sometimes remains as a separate splint called the *hemipterygoid* (penguins, etc.), but it usually disappears, fusing indistinguishably with the palatine. In *Tinamus* the pterygoid articulates with the vomer in the adult as in struthious birds.

The principal foramina are as follows: the condylar foramen for the 12th nerve, through the exoccipital bone slightly in front of and ventral to the foramen magnum. Slightly external to and behind the condylar foramen is the jugular foramen for the 9th, 10th, and 11th nerves and for the internal jugular vein, between the periotic (petrosal) and the exoccipital bones. To the outer side of the jugular foramen is a depression, the tympanic recess, at the median anterior end of which is the opening into the carotid canal for the internal carotid artery. The 7th nerve traverses the periotic bone and emerges by a small foramen in front of the fenestra ovalis. The eustachian canals open into a deep notch at the anterior end of the basitemporal, and just external to these are the anterior openings of the carotid canals. The foramen for the trigeminal is just in front of the articulation of the quadrate and is between the prootic and alisphenoid. The optic foramen is a large foramen in the hinder end of the interorbital septum; and just behind it are two or three small openings for the ophthalmic branch of the 5th, the 3rd, 4th, and 6th nerves. The olfactory foramen is dorsal to the optic and is continued as a groove between the interorbital septum and the frontal.

Huxley\* pointed out the following different arrangements in the palatal bones of birds: In the *Ratitae* and *Tinamus* the vomer is large and broad, and the palatines do not articulate with the rostrum, the vomer intervening; there are well marked basipterygoid processes, which articulate with the hinder parts of the pterygoid; the maxillo-palatines unite with the vomer. This is the *dromaeognathous* arrangement. In *Carinatae* (excepting *Tinamus*) the palatines and pterygoids articulate with the

\* P. Z. S. 1867.

rostrum at the point where they join one another. When the vomer is small and pointed in front (or absent), and the maxillo-palatines do not unite with one another and the vomer, the arrangement is termed *schizognathous* \* (plovers, gulls, penguins, fowls, pigeons, etc.). The *aegithognathous* † arrangement (passerines, swifts) is similar to the *schizognathous* excepting in the fact that the vomer is truncated in front. Lastly when the vomer is small and the maxillo-palatines are large and spongy, uniting with the maxillo-palatines or with each other across the middle line ventral to the vomer the palate is described as *desmognathous* ‡—(anserine birds, birds of prey, parrots, etc.).

In the **vertebral column** (Fig. 239) a long flexible cervical region, a rigid thoracic, lumbar, and pelvic region, and a slightly moveable, short, caudal region may be distinguished.

The cervical and thoracic regions are not sharply distinct from each other, since the cervical vertebrae, as in crocodiles, bear double-headed ribs, the capitulum of which is fused with the centrum and the tubercle with the transverse process, enclosing between them the vertebralarterial canal. The last two cervical ribs are free, but do not reach the sternum. The atlas is a ring-like bone, and the axis possesses a peg-like odontoid process. The articulating surfaces of the remainder of the cervical vertebrae are saddle-shaped and without epiphyses (except in the parrots). The neck is long and freely moveable and contains nine to twenty-three (swan) vertebrae. The thoracic vertebrae are fewer in number; they all carry ribs which are united to the sternum by a sternal portion (*Stc*), and to the vertebrae by a capitulum which is attached to the centrum or lower part of the arch and by a tuberculum to the transverse process of the neural arch. The vertebral portions of the ribs carry backwardly directed bony uncinat processes. The thoracic vertebrae are sometimes slightly moveable upon one another, sometimes ankylosed; in the former case the articulating surfaces are saddle-shaped, or as in the penguins, plovers, etc., are rounded, the anterior surface being convex, the posterior concave.

The rib-bearing thoracic vertebrae are followed by a tolerably extensive region of the vertebral column in which the vertebrae are fused with one another and with the long iliac bones of the pelvic girdle. This is the compound **sacrum** and includes as many as sixteen to twenty or more vertebrae. Of these one or

\* Alluding to the cleft between the maxillopalatine and vomer.

† *ἀιγιθός*, a finch.

‡ *δέσμα*, a bond.

two bear ribs which reach the sternum and are clearly thoracic ; these are followed by a variable number (about six) of vertebrae

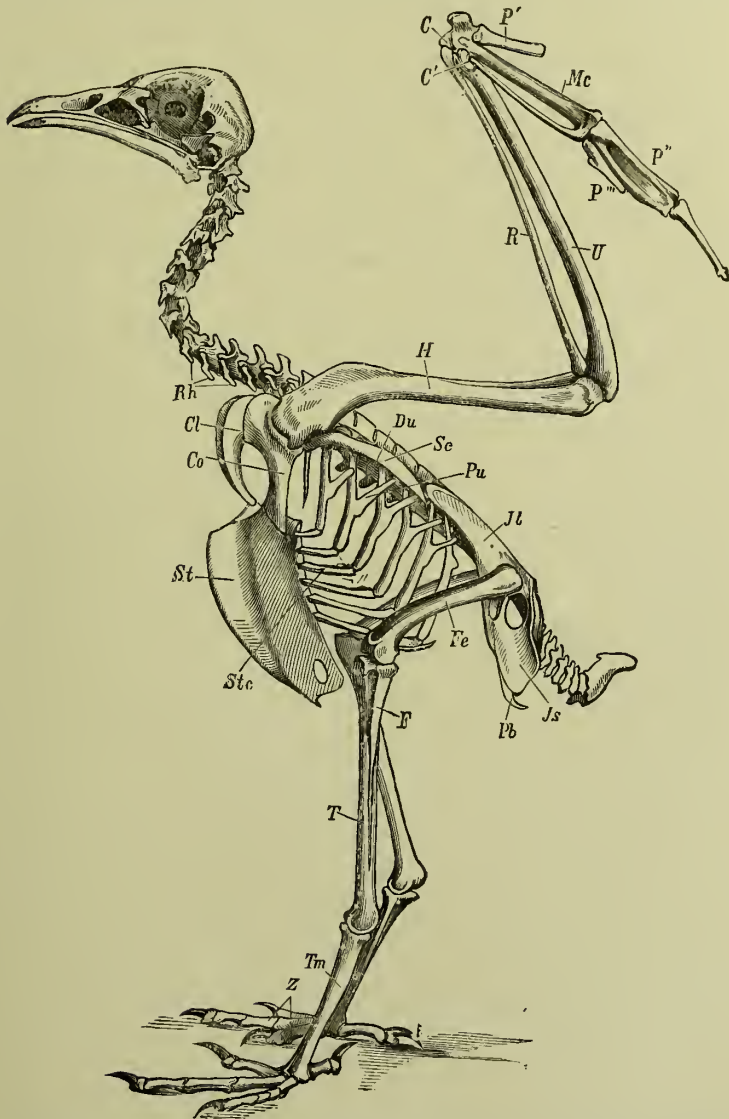


FIG. 230.—Skeleton of *Neophron percnopterus* (from Claus). CC' carpus; Cl clavicle; Co coracoid; Du inferior spinous processes of the thoracic vertebrae; F fibula; Fe femur; H humerus; Jl ilium; Js ischium; Mc metacarpus; P', P'', P''' phalanges of the fingers; Pb pubis; Pu uncinate processes of the ribs; R radius; Rh cervical ribs; Sc scapula; St sternum; Stc sternal portions of ribs; T tibia; Tm tarso-metatarsus; U ulna; Z toes.

which are clearly lumbar (presacral); then follows the true sacrum consisting of two vertebrae with their sacral ribs; finally comes the postsacral portion of the compound sacrum, which consists of from three to seven of the anterior caudal vertebrae. The short **caudal** region, which succeeds the postsacral, consists, as a rule, of from seven to eight moveable vertebrae, of which the last is represented by a vertical, laterally compressed plate, the *pygostyle*, which supports the tail-feathers and the uropygial gland. This deep ploughshare-shaped terminal bone is composed of from four to six fused vertebrae, so that the reduction of the number of caudal vertebrae, as compared with the number in the tail of *Archaeopteryx*, is not very great.

The moveable vertebrae are separated by synovial cavities, each of which is divided into two by a plate of fibro-cartilage, called the *meniscus*. The meniscus is perforated by an aperture which transmits a fibrous cord which is a remnant of the notochord.

The **sternum** (*St*) is a broad bone which covers not only the thorax but a great part of the abdomen and bears a projecting keel-like crest which serves for the attachment of the great pectoral muscles (*Carinatae*). The keel is reduced or obsolete only when the power of flight is feeble or absent (*Ratitae*, *Strigops*). The postero-lateral part of the sternum may be fenestrated, giving rise to vacuities or notches in the bone.

The *spina sternalis* or *rostrum* is the anterior continuation of the sternum between the articulation of the coracoids. In some birds it consists of a dorsal (*spina interna*) and ventral (*spina externa*) portion.

The **pectoral girdle** consists of a scapula, a coracoid, and a clavicle. The scapula (*Sc*) is a sabre-shaped bone lying along the dorsal side of the thoracic framework. Its anterior end is expanded and firmly united by ligament (usually not ankylosed) with the coracoid (*Co*), which is directed ventralwards and articulates with a groove on the anterolateral edge of the sternum. In the *Ratitae* the long axis of the scapula is nearly in the same straight line as that of the coracoid, but in most birds it forms an angle less than a right angle with the coracoid (Fig. 239). Both bones contribute about equally to the glenoid cavity. The glenoidal end of the scapula is produced into an acromial process, to which the clavicle is attached. The clavicle is also

attached to a process—the clavicular process—of the dorsal end of the coracoid. A foramen, called the *foramen triosseum*, is thus left between the three bones of the shoulder girdle at the point where they meet one another. The two clavicles are ankylosed together ventrally and may at this point be attached by ligament or even ankylosed to the keel of the sternum. The clavicles are small and remain distinct from one another ventrally in some birds (parrots, owls, toucan, emeu) and are rarely absent (some Ratitae, some parrots).

The humerus has an expanded head, a preaxial and postaxial tuberosity, of which the postaxial is the larger, and a deltoid ridge which extends for a short distance down the shaft of the bone from the preaxial tuberosity. The pneumatic foramen is on the proper dorsal face of the proximal end of the bone close to the postaxial tuberosity. The ulna is stouter than the radius and often presents a number of tubercles caused by the attachment of the wing quills. The carpus consists of two bones only, but in the young bird it is said that a distal carpal row of three pieces which later fuse with the metacarpus can be made out. Three digits are present, viz. digits 1, 2, and 3. The metacarpals of these are all fused together; that of the pollex is much shorter than the others and carries two phalanges. The metacarpals of the other two digits are united at each end; digit No. 2 has two or three phalanges and digit No. 3 has one phalanx (two in the ostrich). The terminal phalanx of the pollex is often unguiculate, as is in rare cases (ostrich) that of the second digit. In the emeu and apteryx the first and third digits are absent in the adult, and in some birds the wing bones are considerably reduced (*Hesperornis*) and almost or quite absent (Moas). In *Archæopteryx* the metacarpals are separate and all the digits bear claws. In some embryo birds a rudiment of digit No. 4 is said to have been detected.

In the pelvic girdle the ilia are remarkably expanded antero-posteriorly both in front of and behind the acetabulum, and attached by their whole length to the compound sacrum. The ischia are directed backwards parallel to the hinder part of the ilium to which they are attached posteriorly converting the ilio-ischiatic notch into a foramen. The pubes are slender bones directed backwards parallel to the ischia, with which they often unite posteriorly. The pubes and ischia do not unite with each



other ventrally except in the ostrich in which there is a symphysis pubis, and in *Rhea* in which there is a symphysis ischii; but the symphysis ischii of *Rhea* is peculiar in being dorsal to the intestine and ventral to the kidneys; it is associated with a curious weakening of the postsacral part of the vertebral column in the adult. All three bones enter into the acetabulum which is perforated, and the pubis has in some birds (*Apteryx*) a forwardly directed preacetabular process (pectineal process). This process appears to be more marked in embryos, in which it was discovered by Miss Johnson \* in the chick. In a few birds the ilia are quite separate from the ischia except in the acetabulum (*Tinamus*, *Struthio*, *Apteryx*, *Hesperornis*, etc.). The short and powerful femur is directed obliquely horizontally forwards and concealed beneath the flesh and feathers of the abdomen, so that the knee-joint is not visible externally. The head is rounded and stands out at right angles to the bone. A patella is usually present. The crus, which is much longer, is chiefly composed of the tibia, the fibula being reduced (especially distally) and represented by a styliform bone on the outer side of the tibia. The proximal end of the tibia is expanded and has on its anterior face a great ridge, the cnemial crest. There appears to be no tarsus, but two rows of tarsal elements are present in the embryo, of which the proximal row unites with the tibia and the distal with the metatarsus, so that the bone which we have called tibia is really the tibio-tarsus, and the ankle joint is intertarsal. In the same way the metatarsus is in reality a tarso-metatarsus. The tarso-metatarsus varies much in length and is the cause of the differences in the length of the leg. It is composed of the distal tarsalia and of three long metatarsal bones of digits 2, 3, and 4, fused together. At its lower end it discloses its composite nature by dividing into three processes which are provided with articulating surfaces for the proximal phalanges of the corresponding digits. When a fourth toe (digit No. 1) is present, its metatarsus is distinct from the tarso-metatarsus and has the form of a small bone on the inner side of the metatarsus; it carries the phalanges of the inner digit or hallux. The usual phalangeal formula is 2, 3, 4, 5. No bird has digit No. 5,† though a trace of its metatarsal is said to be present in the embryo.

\* *Q.J.M.S.*, 23, 1883, p. 399.

† The fifth digit seen in some breeds of fowl is not the true fifth digit, but an abnormality.

When three toes only are present the hallux is suppressed. In the ostrich digit No. 2 is also absent. In the penguins the fibula has the same length as the tibia, and the metatarsals though fused, are more distinct than in other birds.

In the development of the foot there are said to be at first three proximal tarsals and five distal. The proximal elements unite while still in the cartilaginous condition into one piece which then ossifies and fuses with the tibia. The five distal elements are also said to unite to one cartilage which ossifies and fuses with the second, third, and fourth metatarsals. The latter are at first separate, but later fuse. When the compound metatarsal so formed elongates, as it generally does, the first metatarsal does not share in the elongation but remains distinct at the distal end; in one or two cases (e.g. *Phaethon*) it fuses with the lower end of the tarsometatarsus. A centrale (or sometimes two) is said to be sometimes detectable in the embryo and even to persist in the adult as a distinct bone on the posterior surface of the joint.

The brain of birds (Fig. 240) is much more highly developed than that of reptiles, and completely fills the roomy cranial cavity. The hemispheres are, indeed, still without superficial convolutions. They cover not only the thalamencephalon, but also the two large, laterally displaced corpora bigemina. The differentiation of the cerebellum is still further advanced, since there is a median part corresponding to the so-called vermis of Mammalia and marked by transversely directed sulci and small lateral lobes.

In consequence of the cervical flexure of the embryo the medulla

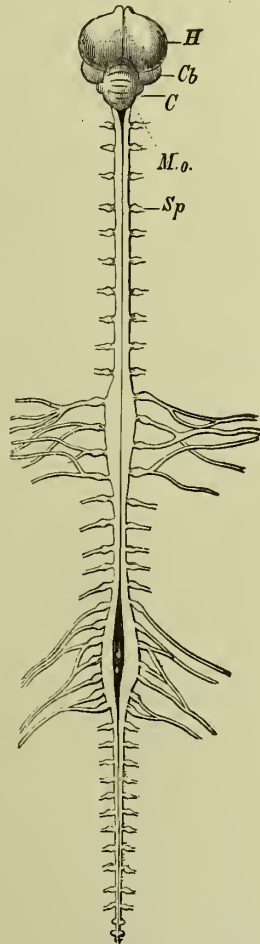


FIG. 240.—Brain and spinal cord of a pigeon. *C* cerebellum; *Cb* optic lobes; *H* cerebral hemispheres; *Mo* medulla oblongata; *Sp* spinal nerves.

oblongata forms an angle with the spinal cord, the posterior columns of which diverge from one another in the posterior

enlargement of the lumbar region so as to form a second sinus rhomboidalis (Fig. 240). The cranial nerves are all separate and their distribution is essentially the same as in the Mammalia. The spinal cord reaches almost to the end of the neural canal of the vertebral column.

**Sense organs.** The eyes always attain a considerable size and a high development. The eyelids are always moveable, especially the lower lid and the transparent nictitating membrane, which is drawn over the eye by a peculiar muscular apparatus. The eyeball (Fig. 241) has an unusual form, in that the hind part on which the retina is spread is a segment of a much larger sphere than is the small anterior part. The two parts are connected

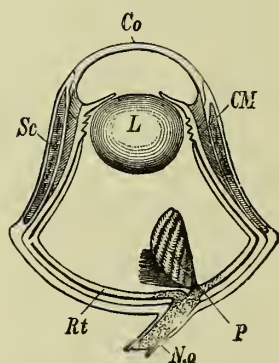


FIG. 241.—Eye of a nocturnal bird of prey (after Wiedersheim). CM ciliary muscle; Co cornea; L lens; No optic nerve; P pecten; Rt retina; Sc ossifications of the sclerotic.

by a median portion, which has the shape of a short truncated cone, with the smallest end directed forwards. This form of the eyeball is most marked in the nocturnal birds of prey, and least in the aquatic birds in which the axis of the eye is short. There is always a bony sclerotic ring behind the edge of the cornea. The cornea is strongly arched, while the anterior surface of the lens only possesses a considerable convexity in nocturnal birds. The pecten (wanting only in *Apteryx*) is a peculiar structure of the avine eye. It

consists of a process of the choroid, which traverses the retina near the optic nerve and passes obliquely through the vitreous humour to the lens. It corresponds to the falciform process of the piscine and reptilian eye. The avine eye is characterised not only by the sharpness of vision consequent on the large size and complicated structure of the retina (many birds possess two foveae centrales in each eye), but also by the highly-developed power of accommodation, which is principally due to the muscle of the so-called ciliary ligament (Crampton's muscle), and also to the great mobility of the muscular iris, which possesses both sphincter and dilator muscles. The sphincter is supplied by the third nerve and is

under the control of the will. Lacrymal and harderian glands are both present. They are placed within the orbit, the former on the outer side of the eyeball and the latter on the inner and upper side. The harderian gland opens within the nictitating membrane. The secretion of both glands is carried off by a wide lacrymo-nasal duct which leaves the inner angle and opens in the nasal cavity immediately above the internal nares.

The auditory organ is contained in the periotic bone. It possesses three large semicircular canals which open into the utricle, and a sacculus which gives off a slightly bent cochlea (lagena) and a ductus endolymphaticus; the latter enters the cranial cavity and ends in the dura mater in a flattened sac. The cochlea is without an organ of Corti. The vestibule has two openings: the fenestra ovalis which is closed by the terminal piece (operculum) of the columella and looks into the tympanic cavity, and a second more rounded opening, the fenestra rotunda, which is closed by membrane only. The eustachian tubes after leaving the bone join to form a short membranous duct, which opens into the pharynx by a median opening. The tympanic cavity also communicates with air-spaces in the neighbouring bones of the skull. Externally the tympanic cavity is closed by a tympanic membrane, to which the long rod-shaped auditory ossicle (columella), corresponding to the auditory ossicles of Mammalia, is fastened. On the outer side of the tympanic membrane there is a short external auditory meatus, the opening of which is often surrounded by a circle of large feathers, and in the owls is overlapped by a cutaneous valve which is likewise beset with feathers, and constitutes a rudimentary pinna.

The olfactory organ has three pairs of turbinal bones in the spacious nasal cavities. The two nasal apertures,\* except in *Apteryx*, lie more or less near the root of the upper beak; sometimes (crows) they are covered and protected by stiff hairs; in the Procellariidae they are elongated into a tube and join one another. A so-called nasal gland usually lies on the frontal bone, more rarely beneath the nasal bone or at the inner corner of the eye; it opens by a simple duct into the nasal cavity.

The sense of taste is connected with the soft base of the tongue

\* In *Phalacrocorax* and apparently in other Steganopodidae the external nostrils are said to be closed in the adult.

which is rich in papillae. The tongue is soft throughout its whole extent only in the parrots. In most other cases it has a firmer covering, and in many cases lends important aid in mastication. In general the tongue as well as the beak may be regarded as a tactile organ. In rare cases (snipe, duck) the beak is the seat of a finer tactile sensibility, owing to the possession of a soft skin rich in nerves and in the end-corpuscles of Vater.

**Alimentary canal.** In spite of great differences in the mode of nourishment the avine digestive organs present a fairly uniform structure; their peculiarities have relation to the power of flight. The jaws are covered by a hard horny sheath (*rhamphotheca*) and transformed into the beak. The *rhamphotheca* is often composed of several pieces \* (compound). True teeth are entirely absent, at least in living birds as opposed to some fossil forms (*Ichthyornis*, *Hesperornis*, *Archaeopteryx*). While the upper beak is formed by the fused praemaxillae, the maxillae and the nasal bones, the lower corresponds to the two rami of the lower jaw, the fused extremities of which are known as the *myxa*. The lower edge reaching from the angle of the chin to the extremity is termed the *gonys*, the edge of the upper beak is the *culmen*, the region between the eye and the base of the beak which is covered by the cere (*ceroma*) is the *lore*. The form and development of the beak vary extremely according to the special mode of subsistence (Fig. 242).

The tongue, which is always moveable, lies on the floor of the buccal cavity. It consists of the horny or fleshy covering of two cartilages attached to the anterior end of the hyoid bone, and serves for deglutition, and frequently for seizing food. The buccal cavity, which in the pelicans is dilated into a large gular sac supported by the rami of the lower jaw, receives the secretion of a number of small salivary glands (sublingual, submaxillary and parotid; in the woodpecker the sublingual glands are large). There is no *velum palati*. The muscular, longitudinally folded oesophagus, the length of which in general depends on that of the neck, frequently possesses—especially in the birds of prey, but also in the granivorous birds—a crop-like dilatation, in which the food is softened (Fig. 243). In the pigeons the crop bears two small round accessory sacs.

The lower end of the oesophagus is dilated into a glandular

\* Lönnberg, *Arkiv för Zoologi*, 1, 1904, p. 479.



proventriculus, which is followed by the wide muscular stomach (gizzard). While the proventriculus has, as a rule, an oval form and is smaller than the gizzard, the gizzard is provided with muscular walls, which are weaker (birds of prey) or stronger (granivorous birds), according to the kind of food eaten. In the granivorous birds the gizzard is excellently adapted for the



FIG. 242.—Forms of beaks (a, b, c, d, k, after Naumann; g, i, m, o, Règne animal; l from Brehm). a *Phoenicopertus antiquorum*; b *Platlea leucorodia*; c *Emberiza citrinella*; *Turdus cyaneus*; e *Falco candicans*; f *Mergus merganser*; g *Pelecanus perspicillatus*; h *Recurvirostra avocetta*; i *Rhynchops nigra*; k *Columba livia*; l *Balaeniceps rex*; m *Anastomus coromandelianus*; n *Pteroglossus discolor*; o *Mycteria senegalensis*; p *Falcinellus igneus*; q *Cypselus apus*.

mechanical preparation of the softened food material by the possession of two solid plates, which form the horny internal wall and work against one another. It contains small stones which the bird swallows to aid in the grinding of the food. The

first loop of the small intestine (corresponding to the duodenum) surrounds the elongated pancreas, the ducts of which (one to three in number), as well as the usually double bile ducts, open in this region. A gall-bladder is usually present. The beginning of the short large intestine is marked by a circular valve,

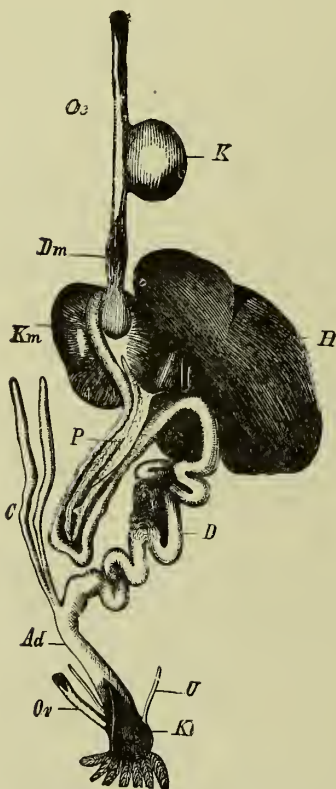


FIG. 243.—Digestive canal of a bird. *Ad* large intestine (rectum); *C* the two rectal caeca; *D* small intestine; *Dm* proventriculus; *H* liver; *K* crop; *Kl* cloaca; *Km* gizzard; *Oe* oesophagus; *Op* oviduct; *P* pancreas placed in the duodenal loop; *U* ureter.

and by the origin of two caeca ; it presents no distinction into colon and rectum, and passes into the cloaca, into which the urinogenital apparatus also opens. At its entrance into the cloaca it presents a sphincter-like circular fold. A peculiar glandular sac—the bursa Fabricii—opens into the dorsal wall of the cloaca. There is no bladder in the adult.

The falciform ligament has a considerable extension, passing back from the pericardium to the hinder part of the body cavity as a median septum. The large omentum is well developed.

The cloaca usually presents three fairly well-marked divisions separated by folds. The anterior of these, often called the *coprodaeum*, is the dilated hind end of the rectum ; its lining is however different from that of the rectum from which it is often separated by the fold above referred to. The middle chamber is called

the *urodaeum* ; it is smaller than the others and receives the openings of the urinogenital ducts. The posterior chamber which opens by the vent, may be termed the *vestibule* (sometimes erroneously called *proctodaeum*) ; it receives the bursa Fabricii dorsally. Most birds are without an organ of copula-

tion, sperm-transference being effected by a slight eversion of the cloaca. In the Ratitae (except *Rhea*) there is solid grooved penis attached to the ventral wall of the vestibular division of the cloaca; it is very similar to the corresponding organ of *Chelonia*, contains erectile tissue and can be extruded or retracted by special muscles. In *Rhea* and anserine birds a very similar organ occurs, but its terminal portion is invaginated during rest and evaginated in erection like the finger of a glove.

The **heart** is completely divided into a right and left half, and lies in the median line, enclosed by the pericardium. As a peculiarity of the heart may be mentioned, the special development of the right auriculoventricular valve, which, unlike the tricuspid valve of the mammalian heart, is a simple strong muscular fold. The left auriculoventricular valve is membranous and possesses chordae tendineæ as in mammals. There is no diaphragm in the mammalian sense and the thoracic cavity is directly continuous with the abdominal. The pulsations of the heart, in correspondence with the more active respiration, are repeated more rapidly than in Mammalia. The right aortic arch alone persists. The carotids converge and run close together in a furrow on the ventral side of the cervical vertebrae. In some birds they unite, and in some only one of them is present. In some cases superficially placed vessels (superficial carotids) coexist with or take the place of the normal carotids (deep carotids). There is no sinus venosus. The veins open by two superior and one inferior vena cava into the right auricle. The renal-portal circulation appears to be absent, all the blood from the hinder part of the body passing either directly into the inferior vena cava or by the coccygeo-mesenteric into the hepatic-portal system. The coccygeo-mesenteric vein is peculiar to birds; starting from the point where the caudal vein bifurcates into the two veins (called variously internal iliacs, hypogastric, renal portal) which run forward on the ventral surface of the kidneys to join the femoral veins, it passes in the mesentery of the rectum to join the portal system as one of the roots of the portal vein; it receives blood from the hinder end of the small intestine, the rectum and the cloaca. There appears to be a representative of the anterior abdominal vein in the form of a vessel which collects blood from the abdominal wall and great omentum and falls into the left hepatic vein; it does not how-

ever anastomose with the system of the femoral as in reptiles and amphibians.

The red blood corpuscles are oval and nucleated.

The lymphatic system opens by two thoracic ducts (ductus thoracici) into the superior venae cavae, but also very generally communicates with the veins of the pelvic region. Lymph hearts are only found at the side of the coccygeal bone in the ostrich and cassowary, and in some wading and swimming birds. They are, however, often replaced by vesicular non-contractile dilatations.

A **spleen**, **thymus**, and **thyroid** glands are present. The thyroid is paired and placed at the base of the neck attached to the carotid artery and jugular vein. The thymus is an elongated body on each side of the neck along the jugular vein. The **supra-renals** (adrenals) are a pair of elongated yellow bodies attached to the ventral surface of the kidneys along the iliac veins.

The **respiratory organs** \* are perhaps the most remarkably modified of all the organs. The lungs are small and but slightly if at all distensible. They are prolonged into a number of thin-walled air-sacs which extend amongst the viscera, into the bones, and sometimes beneath the skin. The organ of voice is not in the larynx but lower down on the trachea, usually at its bifurcation into the bronchi. These peculiarities are associated with three remarkable properties, viz. flight, the extraordinary power of voice production, and the intense activity of the metabolic processes.

The slitlike glossis is placed behind the root of the tongue, and leads into a larynx, which is supported by cricoid, thyroid and arytenoid cartilages, but is devoid of vocal chords. An epiglottis is absent or represented only by a small transverse fold. The trachea is supported by bony rings which are usually complete, and on reaching the thorax bifurcates into the two bronchi. It is not unfrequently longer than the neck, and in such cases, principally in the male sex, is thrown into a number of coils, which either lie outside the thorax beneath the skin (capercally), etc.) or even penetrate into the hollow crest of the sternum (whooper swan).

\* Sappey, *Recherches sur l'appareil respiratoire des Oiseaux*, 1847, and *Compt. Rend.* 22, pp. 250, 508. Huxley, On the respiratory organs of *Apteryx*, *Proc. Zool. Soc.* 1882, p. 560. Strasser, *Jen. Zeitschr.*, 19. pp. 174, 330. Butler, *P. Z. S.*, 1889, p. 452.



**The lower larynx or syrinx.** Except in the ostrich, storks, and some vultures, the vocal organ is placed lower down on the trachea usually at the point where the trachea divides into the bronchi, so that both divisions take part in its formation (Fig. 244). The last tracheal rings and the anterior bronchial rings have a modified form, and are often intimately connected with each other; the end of the trachea and the beginning of the bronchi are compressed or dilated into a vesicular form and transformed into the so-called *tympanum*, which in the males of many ducks is dilated into unsymmetrical secondary cavities (tympanic cavity and labyrinth), which serve as a resonating apparatus. The part of the trachea from which the bronchi

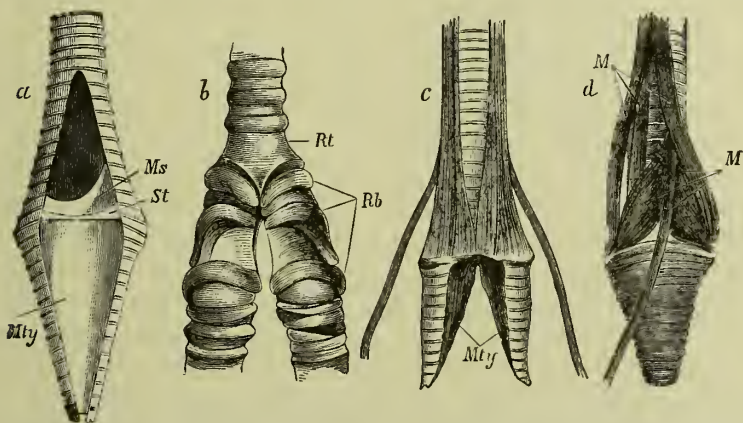


FIG. 244.—Lower larynx of raven (from Owen). *a* side view of larynx laid open; *b* larynx after removal of muscles; *c* larynx with muscles from the front; *d* from the side. *M* muscles; *Ms* membrana semilunaris; *Mty* membrana tympaniformis interna; *Rb* the modified three first bronchial rings; *Rt* modified last tracheal ring; *St* pessulus.

pass off (i.e. tympanum) is traversed in a horizontal direction by a projecting osseous band—the *pessulus*—which forms a vertical septum between the anterior apertures of the two bronchi. This septum, at its anterior (ventral) and posterior (dorsal) ends, gives off on each side two arched processes, which pass downwards—one along the dorsal, and the other along the ventral edge of the bronchus of its side; and between these cornua the internal wall of each bronchus, which is here membranous, is stretched, and constitutes the *membrana tympaniformis interna*. In the singing birds (*Oscines*) there is, in addition, a semi-lunar fold (*membrana semilunaris*) on the pessulus, as a prolongation



of the *membrana tympaniformis interna*. In many cases a membranous fold—the *membrana tympaniformis externa*—is developed on the external side of the tympanum, and forms with the free edge of the internal tympaniform membrane (i.e. with the *membrana semilunaris*), a vocal slit or glottis on either side. The tension of these folds, which function as vocal chords, is regulated by a muscular apparatus, which connects the trachea with the lateral parts of the tympanum, or also with the anterior bronchial rings, and is most highly developed in the singing birds, in which the syrinx may possess five or six pairs of such muscles. This is the usual form of syrinx. It is occasionally placed at the lower end of the trachea or at the upper end of the bronchi; in such cases its structure though essentially as described presents some modifications.

The bronchi are relatively short and lead, at their entrance into the lungs, into a number of wide membranous bronchial tubes, which traverse the pulmonary tissue. The lungs which are of relatively small bulk are not, as in mammals, freely suspended in a closed thoracic cavity and invested by a pleural sac, but are attached to the dorsal wall of the body cavity by cellular tissue, and sunk in the interspaces between the ribs at the sides of the vertebral column. The behaviour of the bronchial tubes and the structure of the finer respiratory air-spaces of the lungs present essential differences from those of the Mammalia. The air-sacs are expansions of the blind ends of some of the main bronchial tubes; they have thin, somewhat stiff membranous walls, and project for the most part into the general body-cavity. There are five pairs of them, called, in order from before backwards, the cervical (prebronchial), the interclavicular (infra-bronchial), the anterior thoracic (anterior intermediate), the posterior thoracic (posterior intermediate) and the abdominal (posterior). The main bronchus enters the lung of its side on the ventral surface a short distance from the anterior end. It is continued as the *mesobronchium* through the lung to its hind end where it dilates into the large abdominal air-sac (Fig. 245, *La*) which lies along the dorsal wall of the body-cavity in the pelvic region on the ventral side of the kidneys, to which and to the adjacent walls of the pelvis its dorsal wall is adherent ventrally it is covered by peritoneum and is in contact with the coils of the intestine.

The mesobronchium \* a short distance before its termination in the abdominal air-sac gives off a branch which passes to the lung surface and dilates into the posterior thoracic air-sac. This lies on the outer side of the anterior end of the abdominal sacs on the ventral side of the hind end of the lung and behind the lung. Its outer side is united with the side wall of the posterior part of the thorax and of the anterior part of the abdomen, and the anterior part of its dorsal wall with the lung surface. Mesially the anterior dorsal end of it is in contact with its fellow (forming part of the median septum, see below). The tubes which pass to the other air-sacs are secondary bronchi and are called *entobronchia*; they come off from a dilatation on the mesobronchium, called the *vestibule*, soon after it enters the lung. There are four entobronchia. The fourth runs to the hind end of the lung and ends there caecally. The third runs parallel with this; it gives off close to its point of origin from the vestibule a tube which immediately dilates into the anterior thoracic sac. This lies on the ventral surface of the middle part of the lung to which its dorsal wall is adherent and extends back so as to overlap the outer side of the anterior part of the posterior thoracic sac. Its outer wall is adherent to the side walls of the

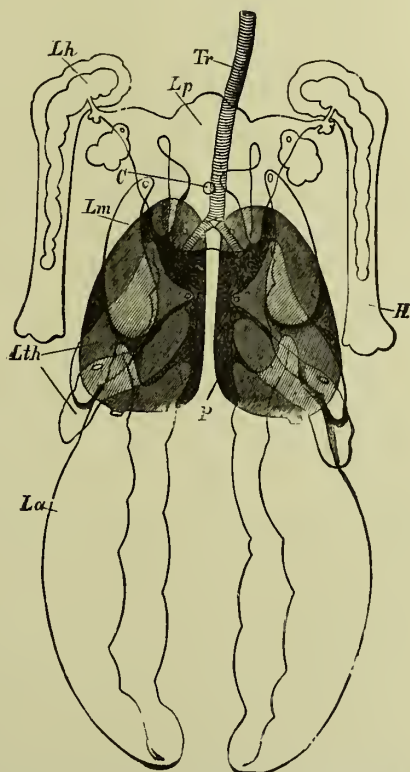


FIG. 245.—Lungs and air-sacs of the pigeon (diagrammatic, after C. Heider). *C* connection of the interclavicular sac with the sternal air-spaces; *La* abdominal air-sacs; *Lp* median part (peritracheal) of interclavicular air-sac with its diverticula (*Lh*) into the humerus (*H*) and between the pectoral muscles (*Lm*); *Lth* thoracic air-sacs; *P* lungs; *Tr* trachea.

vestibule a tube which immediately dilates into the anterior thoracic sac. This lies on the ventral surface of the middle part of the lung to which its dorsal wall is adherent and extends back so as to overlap the outer side of the anterior part of the posterior thoracic sac. Its outer wall is adherent to the side walls of the

\* The following description of the bronchi refers mainly to the pigeon.

thorax, and its inner walls are in contact with the pericardium, except anteriorly and dorsally where it is adherent to its fellow (forming part of the median septum).

The second entobronchium gives off a wide branch which passes to the interclavicular sac and is joined just where it opens into this sac by a branch from the first entobronchium. The posterior part of the interclavicular air-sac lies on, and its dorsal wall is united with, the ventral surface of the anterior part of the lung; this part overlaps the anterior part of the anterior thoracic. The anterior part is united with its fellow and surrounds the hinder end of the trachea between the two clavicles; it gives off lateral diverticula one of which passes outwards behind the coracoid and dilates into a large axillary chamber near the shoulder joint which communicates with the air-cavities in the humerus.

The first entobronchium is directed forwards and, after giving off the tube to the interclavicular sac already mentioned, is continued to the anterior end of the lung, where it opens into the small cervical sac, which lies in front of the lungs at the base of the neck and dorsal to the anterior part of the interclavicular sac. It lies between the *longus colli* muscle with the vertebral column dorsally and the oesophagus and bronchus ventrally, and is widely separated from its fellow. In many birds the cervical air sacs are continued up the neck close to the ventral sides of the vertebrae communicating with the air-cavities in these structures and in front with the air-cavities in the bones of the upper beak.

The communications (*ostia*) on the surface of the lungs by which the secondary bronchi communicate with the air-sacs are for the most part well-marked openings. The ostia of the abdominal sacs are at the postero-external angle of the lung; those of the posterior thoracic just anterior and external to the last; those of the anterior thoracic are nearer the middle line not far behind the entrance of the main bronchus into the lung; those of the interclavicular are just anterior to the entrance of the main bronchus, and the cervical air-sacs are given off from the anterior end of the lung.

The ventral surface of the lungs is invested by a thin fibrous membrane called the *pulmonary aponeurosis* which is perforated by the ostia of the air-sacs. This membrane is continuous in the middle line with a median *vertical septum* which separates the

lungs of the two sides and is continued a little ventral to the lungs by the opposed median walls of the thoracic air sacs (see above). The outer edges of the pulmonary aponeurosis are inserted into the thoracic wall at the edge of the lung, and the posterior part of it contains muscles which arise from the vertebral parts of the ribs. The dorsal walls of the interclavicular, anterior thoracic air-sacs, and of a small part of the posterior thoracic sacs, and possibly of a small part of the anterior region of the abdominal air-sacs are adherent to this aponeurosis. The pulmonary aponeurosis has been compared to the mammalian diaphragm, but it is very doubtful if this homology can be maintained, for it does not cut off the whole of the lung from the body cavity, the air-sacs extending through it, and the pericardium lies altogether outside it.

However this may be, there can be no question that the so-called *oblique septum* has nothing to do with a diaphragm with which it also has been compared. Indeed the oblique septum which is described by authors as dividing the body cavity into a dorsal pulmonary part and a ventral visceral part, containing the pericardium and viscera, has no separate existence. It consists merely of those parts of the walls of the interclavicular and thoracic air-sacs, and possibly also of the anterior end of the abdominal, which are not adherent to the body wall, to the lung surface, or to each other, i.e. it consists mainly of the ventral walls of these sacs, and does not divide the body cavity at all, there being no portion of that cavity dorsal to it.

The abdominal sacs lead into the cavities of the femora and pelvic bones, while the interclavicular sacs are prolonged into the air-spaces of the bones of the arm, and may extend into the sternum and into the pectoral muscle. The extensions of the cervical sacs have already been referred to. In many birds the extensions of the air-sacs are much greater than those described. In some they send extensions beneath the skin. In some of the large swimming birds the cutaneous prolongations are so numerous that the skin emits a crackling sound when touched. The pneumaticity of the bones has been already referred to. It is greatest in the screamers and hornbills, in which all the bones are pneumatic and an extensive system of subcutaneous air-sacs exists. The air-cavities in the bones of the head are diverticula of the nasal passages, tympanic cavity, etc.

The mesobronchium and secondary bronchi (entobronchia) give off tertiary bronchi (parabronchia) which sometimes anas-

tomose. The tertiary bronchi give off the fine canaliculi through the walls of which the respiratory exchanges take place.

From the above account it becomes quite clear that the mechanism of respiration of birds must be quite different from that of mammals. In birds, when the thorax and abdomen dilate, air rushes, not into the lungs, which being but slightly distensible are but little affected, but right down the main bronchi into the air-sacs. These therefore act as reservoirs of air which affects by diffusion the composition of the air in the peripheral extensions of the air-sacs, and of the air in the ultimate pulmonary passages, which latter must be almost entirely of the nature of what physiologists call residual air.

The rate of respiration in birds is considerably greater than in mammals. But whereas in mammals the tidal air, i.e. the air taken in and given out in each inspiration and expiration, is only renewed once by each respiratory act, i.e. by inspiration, in birds it is renewed twice; for the air in the bronchial passages is renewed in inspiration from the outside, and again in expiration by the unvitiated air of the air-sacs. It follows therefore that each respiratory act is practically twice as effective in birds as it is in mammals. It seems clear then that the respiratory mechanism of birds is a much more efficient apparatus than that of a mammal and that the oxidation of the blood must be much more complete. This is what we should expect when we remember the much greater activity of birds, and the wonderful way in which they are able to combine intense muscular action with the most remarkable production of voice.

The exact means by which the thorax and abdomen are dilated and compressed in the act of respiration are not fully understood. But having regard to the fact that in a bird the air-sacs are always found distended after death, it seems probable that under ordinary circumstances expiration is a muscular action, by which the thorax and abdomen are diminished in size, and that inspiration is a purely passive action due to the rebound of the thoracic framework and abdominal wall, in virtue of their elasticity, after the muscular tension is relaxed. Whether the backbone is raised or the sternum lowered in this rebound no doubt depends upon what the bird is doing. If it is standing, the sternum will be lowered, while on the other hand if it is supported on its wings in flight the backbone will be raised.



The large elongated **kidneys** are placed in the excavations of the sacrum between the transverse processes, and are divided by indentations into a number of lobes (usually three). The ureters run backwards and open into the middle chamber of the cloaca internally to the genital aperture. The urinary excretion is not liquid, as in Mammalia, but is a white semifluid mass which contains a considerable quantity of urates. The absence of water in the urine of birds is a remarkable fact. In mammals the nitrogenous waste comes away in solution, which causes a considerable loss of water from the blood. In birds, in which this loss does not take place and in which there are no sweat glands, loss of water must be mainly confined to the internal surface of the air passages. No doubt the evaporation which takes place on the very extensive internal air-passages and sacs is an important factor in the regulation of the body temperature.

The **generative organs** closely resemble those of the Reptilia. The males are generally distinguished, not only by their superior strength, but also by the brighter colour of their plumage and the greater power of their song. There are two oval testes at the anterior end of the kidneys; they become much enlarged at the breeding season, and the left is usually the larger. The epididymis, which is but little developed, leads into the vas deferens, which passes back along the outside of the ureter. The ends of the vasa deferentia are frequently swollen so as to form seminal vesicles, and open on two conical papillae placed on the hinder (dorsal) wall of the cloaca.

A copulatory organ is, as a rule, wanting; in some of the larger water birds, however (*Ciconia*, *Platalea*, etc.) a rudimentary penis is present as a wart-like process on the front (ventral) wall of the cloaca. It is larger in most of the Struthionidae, the ducks, geese, swans, and in the curassows and guans (*Penelope*, *Urax*, *Crax*). In these birds a curved tube, supported by two fibrous bodies, is attached to the ventral wall of the cloaca. The end of the tube can be retracted by an elastic band. A superficial groove serves to conduct the sperm during copulation. In the ostrich, the penis attains a still higher structure, analogous to that of the male copulatory parts of the Chelonians and Crocodilia. Below the two fibrous bodies, the broad bases of which arise from the front wall of the cloaca, there is a third cavernous body the extremity of which is non-retractile and

passes into an erectile bulb—the rudiment of a glans penis.

In the female generative organs the ovary and oviduct of the right side are reduced or entirely absent. The generative organs of the left side, however, are correspondingly larger at the breeding season. The oviduct is much coiled, and is divided into three regions : (1) The wide abdominal ostium in front ; (2) the coiled glandular part which secretes, from the glands of its longitudinally folded mucous membrane, the albumen which is added in layers and is twisted together at the ends to form the chalazae ; (3) a posterior short and wide portion—the so-called uterus—which serves to produce the variously coloured egg-shell, and

opens by a short and narrow terminal region into the cloaca on the outer side of the corresponding ureter. When there are copulatory parts in the male, there are also clitoris-like structures at the same place in the female.

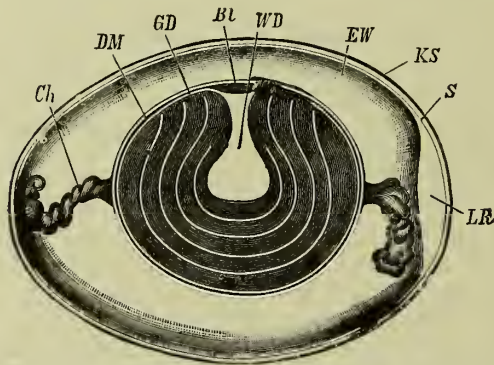


FIG. 246.—Diagrammatic longitudinal section through an undeveloped hen's egg (after Allen Thomson). *BL* germinal disc; *Ch* chalazae; *DM* vitelline membrane; *EW* albumen; *GD* yellow yolk; *KS* calcareous shell; *LR* air-chamber; *S* shell membrane; *WD* white yolk.

Nothing seems to be known as to the actual process of copulation in birds.

**Development.**—Birds are, without exception, oviparous. The egg is remarkable for the large amount of yolk (distinguishable into white and yellow yolk), and its porous calcareous shell (Fig. 246). The development requires a high temperature, at least equal to that of the blood. The necessary heat is usually supplied by the bird during incubation.

Fertilization takes place in the upper region of the oviduct before the secretion of the albumen and of the shell membrane, and is at once followed by the partial (discoidal) segmentation (Fig. 247) which only implicates the clear part of the yolk (formative yolk) around the germinal vesicle—the germinal disc or so-called tread of the cock (*cicatricula*).

When the egg is laid, the segmentation is already completed and the cicatrícula has developed into the blastoderm. The embryo, which later projects from the yolk, develops, as in reptiles, the characteristic foetal membranes—the amnion and allantois. The duration of the embryonic development varies according to the size of the egg and the relative development of the young when hatched. The bird, when ready to come out, breaks the blunt end of the shell by means of a sharp tooth placed at the extremity of the upper beak.

The young when hatched have essentially the organisation of the adult animal, although they may be still far inferior to it in the degree of their bodily development. While the Galli, Limicolæ, Lari, Ratitæ, etc., have when hatched a complete covering of down, and are so far advanced in development, that they at once follow the mother on land or into water and there seek their own food (*præcoces*); others like the Passeres, Columbinae, etc. leave the egg membranes very early (*altrices*); they are naked, or only covered with down in places, and incapable of free locomotion or of feeding themselves, and remain for some time in the nest, in which they are fed and tended by their parents.

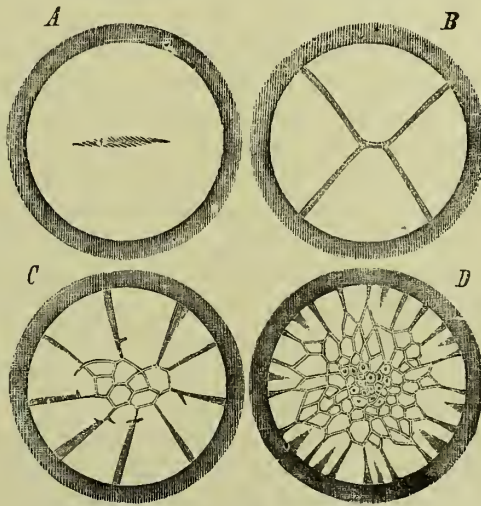


FIG. 247.—Segmentation of the germinal disc of a fowl's egg; surface view (after Kolliker, from Claus). *A* germinal disc with the first vertical furrow. *B* the same with two vertical furrows crossing one another at right angles. *C* and *D* more advanced stages with small central segments

The mental qualities of birds are incomparably higher than those of reptiles. The higher development of the senses (sight) renders them capable of a sharp discernment, with which is combined a good memory. Under the guidance of its parents the young bird in some instances learns to fly and sing; it

collects experiences, which it combines so as to arrive at judgments and conclusions ; it recognises the surroundings of its nest, distinguishes between friends and foes, and selects the proper means both for the preservation of its existence and for the care of its brood. In some birds the capacity for profiting by instruction and the faculty of imitation are extraordinarily developed (starling, parrot). The emotional side appears no less developed, as may be inferred not only from their general behaviour and the varying expression of their song, but especially from the behaviour of the two sexes at the breeding season. Their instinctive actions are directed to the preservation of the individual, and as in insects, but in a far higher degree, to the care of their offspring.

In general the manifestations of intelligence as well as of instinct attain their maximum at the time of reproduction, which in the temperate and colder climates usually takes place in the spring (in the crossbill at almost any time of the year). The voice is clearer and richer in the breeding season ; the male endeavours to excite the female by his song and the beauty of his plumage. In addition to the changes of plumage and song, the whole behaviour of birds is modified under the influence of sexual excitement (love-gestures, etc.).

Most birds build nests, and seek for this purpose a suitable place in the district they inhabit. Only a few birds (goat-suckers, stone-curlew, Alcidae) make no sort of nest, but those which breed on the ground (Laridae, Limicolae, Galli, and Ratitae) scoop out a pit or make a depression in moss and grass. The most skilfully constructed, however, are the nests of those birds which glue particles of extraneous matter together with their sticky saliva or which weave fine tressworks of moss, wool and grass-stalks (weavers). As a rule it is the female alone which builds the nest, the male merely helping in collecting the materials. There are, however, instances in which the male takes a share in the construction (swallows, weavers) ; while in other cases (Galli, chaffinch) the male takes no share at all in building the nest. Many sea-birds, as the auks and penguins, lay but one egg, and most of the large birds of prey, pigeons, and humming-birds, lay two eggs. The number of eggs is larger in the singing birds and still greater in the swimming birds of ponds and rivers, and in the fowls and ostriches. The duration



of the period of incubation is equally various ; it seems to depend upon the size of the egg and the degree of development of the young when hatched.

Incubation essentially consists in keeping the eggs at a warm, uniform temperature ; this is effected by the body of the sitting bird, and is often facilitated by the presence of naked places on the body. As a rule, the mother alone sits, and the male occupies himself with bringing her food. Not unfrequently, however, as in the pigeons, lapwings, and many swimming birds, the two parents relieve one another regularly, and in many *Limicolæ* the male seems to do all the sitting. In the ostrich the female alone sits during the first period of incubation ; later the parts are changed, and the male undertakes the chief part of the incubation, especially sitting almost all night. The behaviour of the cuckoos of the Old World and certain grackles (*Molobrus*) of the New is very remarkable ; they leave the building of nests and the care of their brood to other birds, and place their small eggs, singly, amongst the eggs of various birds.

Leaving out of consideration the activities which relate to reproduction, the instinct of birds manifests itself, principally in late summer and autumn, as an impulse to migrate, and still more mysteriously as a true guide on the journey. Few birds of the colder and temperate climates pass the winter in the places where they breed (resident birds). Many of them rove over larger and smaller regions in search of food. Others migrate before the beginning of the cold season of the year, when nourishment is deficient, from the northern climates to the temperate, from these to southern regions. In the majority of cases when a bird is resident as a species, it is migratory as an individual. It is also to be noted that a vast number of birds ordinarily strictly diurnal in their habits, chiefly if not always migrate by night.\*

There are but scanty materials for the geological history of this class. The oldest known bird—*Archaeopteryx* of the Jurassic formation—is typically avine. From the Cretaceous, remains of toothed, swimming and wading birds are known (*Hesperornis*, *Ichthyornis*, etc.). In the Tertiary Period the remains are more numerous and belong to groups now existing.

More than 12,000 species of birds have been described. The

\* See Reports of the Migration Committee of the British Association.



differences between many of them are slight and the classification presents considerable difficulties.

The system here adopted, which in its main feature is that of Fürbringer and Gadow, is as follows :—

Order 1. **ARCHAEORNITHES.**

Order 2. **NEORNITHES.**

Sub-order 1. **Ratitae.**

„ 2. **Odontolcae.**

„ 3. **Carinatae.**

- |       |     |                           |
|-------|-----|---------------------------|
| Tribe | 1.  | <i>Ichthyornithes.</i>    |
| „     | 2.  | <i>Colymbiformes.</i>     |
| „     | 3.  | <i>Sphenisciformes.</i>   |
| „     | 4.  | <i>Procellariiformes.</i> |
| „     | 5.  | <i>Ciconiiformes.</i>     |
| „     | 6.  | <i>Anseriformes.</i>      |
| „     | 7.  | <i>Falconiformes.</i>     |
| „     | 8.  | <i>Tinamiformes.</i>      |
| „     | 9.  | <i>Galliformes.</i>       |
| „     | 10. | <i>Gruiformes.</i>        |
| „     | 11. | <i>Charadriiformes.</i>   |
| „     | 12. | <i>Cuculiformes.</i>      |
| „     | 13. | <i>Coraciiformes.</i>     |
| „     | 14. | <i>Passeriformes.</i>     |

It must not be supposed that the divisions here called orders, and sub-orders at all correspond in value with the similarly named divisions in other classes ; for as already pointed out (p. 417) the differences between them are hardly if at all greater than those which distinguish families in other classes of Vertebrata.

Order 1. **ARCHAEORNITHES (SAURURAE).**

This order contains only one genus, the extinct *Archaeopteryx* v. Meyer from the lithographic slates of Solenhofen (Upper Jurassic).

*Archaeopteryx* is the oldest known bird and possesses most of the features of avine specialisation. The peculiar characters

are as follows : Teeth, embedded in sockets, are present in both jaws (Fig. 249). The manus has three clawed digits and the metacarpal bones are separate from one another. The digits

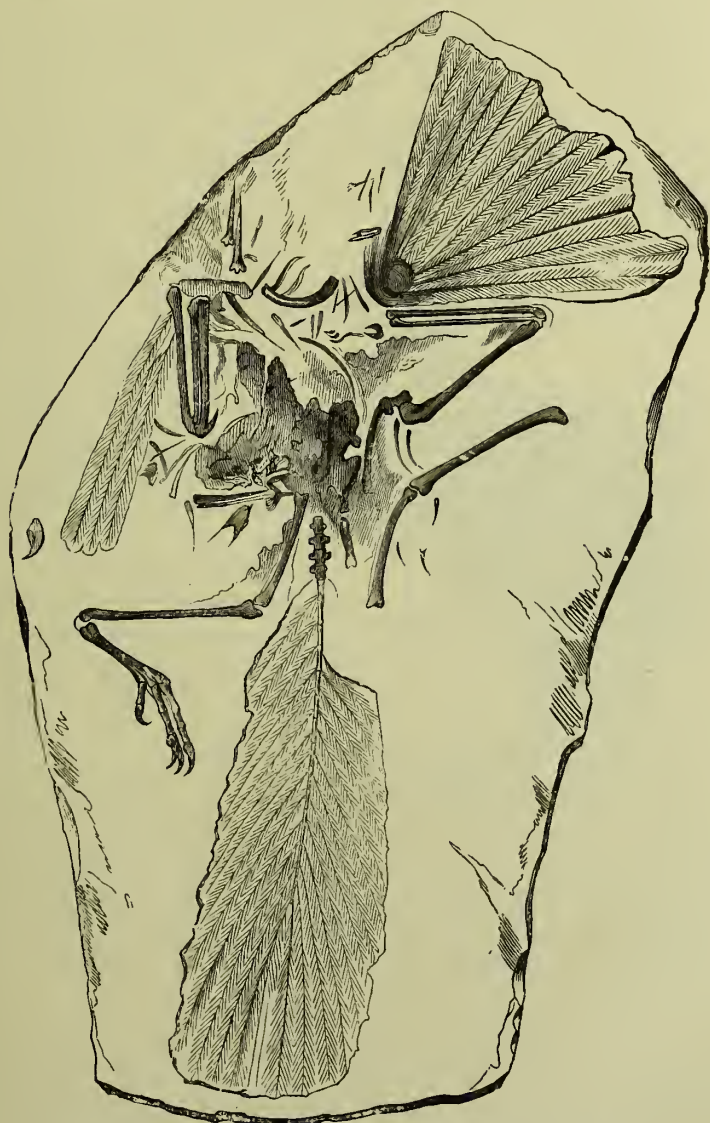


FIG. 248.—*Archaeopteryx lithographica* (from British Museum specimen).

are supposed to be the same as those present in living birds, and possessed two, three, and four phalanges respectively. There is a long tail composed of about twenty separate vertebrae which carry the rectrices on each side (Fig. 248).

The vertebrae appear to be amphicoelous, and the ribs are devoid of uncinate processes. Abdominal ribs appear to have been present.

The beak is short and blunt, and a circle of sclerotic plates is present (Fig. 249). The sternum is not well preserved. The scapula and coracoid appear to have been inclined to one another, and the clavicles are united into a U-shaped bone. The pelvic bones are separate at the acetabulum, and the preacetabular portion of the ilium is shorter than the postacetabular. The hind limb is avine with four clawed digits, the phalangeal

formula of which is 2. 3. 4. 5. The hand carries six, and the ulna ten remiges. The rectrices are arranged in pairs and are attached to the caudal vertebrae (Fig. 248).

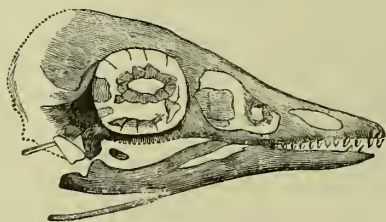


FIG. 249.—Skull and lower jaw of *Archaeopteryx macrura*, Berlin specimen, right side, nat. size (from S. Woodward, after Dames).

*Archaeopteryx* appears to have been of about the size of a rook. Two fairly complete specimens are known,

of which one is in the British Museum and the other at Berlin.

## Order 2. NEORNITHES.

The Neornithes includes all other birds known. The metacarpals are fused with one another; the thoracic ribs have uncinate processes (except in the Palamedeidae); the tail is much reduced in length and the last five or six of the caudal vertebrae are usually united to form a pygostyle. They are divided into three sub-orders, viz. *Ratitae*, *Odontolcae*, *Carinatae*.

### Sub-order 1. RATITAE.

The ratite birds differ from all others in the combination of the following peculiarities: (1) The sternum is devoid of a keel. (2) The long axes of the adjacent parts of the scapula and coracoid are nearly parallel or identical. (3) The posterior ends of the palatines and the anterior ends of the pterygoids are very imperfectly, or not at all, articu-

lated with the basisphenoidal rostrum, being usually separated from it, and supported, by the broad, cleft, hinder end of the vomer (dromaeognathous). (4) Strong basipterygoid processes, arising from the body of the basisphenoid and not from the rostrum, articulate with facets which are situated nearer the posterior than the anterior ends of the inner edges of the pterygoid bones. (5) The upper articular head of the quadrate bone is not divided into two distinct facets. (6) The barbs of the feathers are disconnected, the barbules being without hooks. (7) There is no syrinx. (8) The wings are reduced in size, there is no pygostyle and no oil gland, and the uncinat processes of the ribs are small or absent.

The plumage covers the whole body with tolerable uniformity, except that there are naked places on the head, the neck, the extremities, and the abdomen. It does not present any regular arrangement of pterylae.

The down is much reduced, but the contour feathers have a down-like appearance on account of their flexible shaft and lax vane, or they may be stiff and hairlike, with setiform barbs, or sometimes, as in the wings of the cassowary, they are spinelike. The rhamphotheca is composed of several pieces. There is a large penis and the young are praecoces. Fossil remains are not numerous; the oldest are those of *Struthio* from the Upper Miocene of the Siwalik Hills, etc. The other genera do not for the most part go back beyond the Pleistocene.



FIG. 250.—*Apteryx oweni* (from Claus).

Fam. 1. **Struthionidae.** Ostriches. With

naked head and neck, pubic symphysis, and long, naked legs. The maxillopalatines articulate with facets on the sides of the vomer; the vomer is short and does not articulate either with palatine or pterygoid. The pes has only two digits, viz. Nos. 3 and 4. The feathers are without an aftershaft. They inhabit the plains and deserts of Africa and Arabia. They live in companies and are polygamous. The cock undertakes the greater part of incubation. *Struthio camelus* L.

Fam. 2. **Rheidae.** With partially feathered head and neck, with three-toed feet, and with ischiadic symphysis. The palate is dromaeognathous. The feathers have no aftershaft. South America. *Rhea americana* Lam., the rhea.

Fam 3. **Casuariidae.** With high almost compressed beak, and usually

with a helmet-shaped bony knob on the head; with short neck, and three-toed feet. The palate is dromaeognathous. The feathers have an aftershaft as large as the main shaft. The vomer is large, articulating with the palatines and pterygoids. The wings are very small. They are confined to the Australian Region. *Casuarinus* L., cassowary, New Guinea, North Queensland, and some islands of Papuasias. Most species with bony helmet-like knob on the head, and with brightly-coloured naked lobes on the head and neck. About 6-10 species. *Dromaeus* Gray, emeus. Without helmet or cutaneous lobes. Confined to the Australian continent, and formerly in Tasmania. *D. novae hollandiae* Gray.

Fam. 4. **Apterygidae.** Kiwis (Fig. 250). Small, four-toed birds, with short neck, long weak beak having the nostrils near the extremity. The palate is dromaeognathous. The feathers have no aftershaft. The eyes are remarkable for their small size. These birds, which are about the size of a large hen, are entirely covered with long, hairlike feathers which hang down loosely and completely hide the very small, practically functionless wings. The short powerful legs are covered with scales; the three anteriorly directed toes are armed with claws for scratching; the hind toe (No. 1) is short and raised above the ground. The kiwis are nocturnal birds, which by day remain concealed in holes. They feed on insect larvae and worms, live in pairs, and at the breeding time they lay in holes scraped in the earth a strikingly large egg, which according to some is incubated by the male, and according to others by the male and female in turn. They are confined to New Zealand. *Apteryx mantelli* Bartl., North Island; *A. australis* Shaw, South Island; *A. oweni* Gould, both islands (Fig. 250).

Fam. 5. **Dinornithidae.** Moas. This is a second group of terrestrial birds of New Zealand, which were incapable of flight. It includes a number of forms which are wholly extinct, and some of which attained an enormous size (up to ten feet high). Of heavy, unwieldy build, and incapable of raising themselves from the ground, they were unable to resist the pursuit of the natives of New Zealand. The remains of some have been found in the Pleistocene, and in some cases the bones appear so recent, that it cannot be doubted that they co-existed with man. The traditions of the natives about the gigantic Moa, and numerous discoveries of the fragments of eggs in caves, also point to the fact that these gigantic birds have lived in comparatively recent times. The restoration of the skeleton of gigantic species (*Palapteryx ingens*, *Dinornis giganteus*, *elephantopus*, etc.) has been effected from the bones which have been collected. The wing bones appear to have been absent; the hind limbs are large and massive; the hallux is sometimes present. They are confined to New Zealand and no remains are known older than the Pliocene.

Fam. 6. **Aepyornithidae.** Recently extinct large birds from Madagascar, with long, stout four-toed legs, very small sternum and wings, and very large eggs. *Aepyornis*.

## Sub-order 2. ODONTOLCAE.

Extinct marine flightless birds without sternal keel, with teeth implanted in grooves in the jaws. *Hesperornis* Marsh. Upper Cretaceous of Kansas. A highly specialised diving bird. The wing-bones are much reduced, the humerus only is known; the clavicles are not



united. The teeth are found all along the lower jaw, but are confined to the maxilla in the upper jaw. The palatal structure is not fully known, but there are no basipterygoid processes; the head of the quadrate is single. The vertebral centra are saddle-shaped, and the



FIG. 251.—*Hesperornis regalis*,  $\frac{1}{2}$ . U. Cretaceous, Kansas (from S. Woodward, after Marsh).

bones of the pelvis are free posteriorly. There is no pygostyle *Enaliornis* from the Cambridge Greensand, and *Baptornis* from the North American Cretaceous are probably here.

The so-called **Stereornithes** include a number of large extinct land birds, the skeletons of which have been found in the lower Tertiaries of South

\* Andrews, *Ibis*, 1896, p. 1. Lydekker, *Ibis*, 1893, p. 40, and Dictionary of Birds, p. 904.

America. They are probably not a natural group,\* but include forms which properly belong to different tribes of the Carinatae. The principal genera are *Phororhacos*, *Brontornis*, *Stereornis*, *Patagornis*, *Dryornis*.

### Sub-order 3. CARINATAE.

This sub-order includes the great majority of birds. In the skull the palatines and pterygoids articulate with the basisphenoidal rostrum at the point where they join one another, and the head of the quadrate is double or has two articular facets; basipterygoid processes are present or absent. The sternum is keeled except in the flightless forms (*Didus*, *Stringops*, etc.). The coracoid and scapula meet at nearly a right angle. The barbules carry hooks.

#### Tribe 1. ICHTHYORNITHES.

Extinct, toothed birds with amphicoelous vertebrae and well developed wings; the teeth are implanted in sockets; from the Middle and Upper Cretaceous of Kansas. *Ichthyornis* Marsh, a bird of powerful flight; with teeth all along the lower jaw, but confined to the maxilla in the upper jaw; the head of the quadrate is single as in Ratitae and Odontolcae. A pygostyle is present.

#### Tribe 2. COLYMBIFORMES. Divers and grebes.

Water-birds with webbed or lobed toes and flattened metatarsus. Body carried upright, feet far back. Tail feathers short. Nestlings with complete covering of down. Feathers with aftershaft. Aquintocubital. Holorhinal with nares perviae. Schizognathous, without basipterygoid processes.

Fam. *Colymbidae*. Divers. Marine birds breeding on the shores of inland waters, two eggs; periarctic. *Colymbus glacialis* L., great northern diver.

Fam. *Podicipedidae*. Grebes. Body short, they construct nests of water weeds; the young use their wings as fore-feet; cosmopolitan except in arctic and antarctic regions. *Podiceps cristatus* L., great crested grebe.

#### Tribe 3. SPHENISCIFORMES, Penguins.

Flightless marine birds with anterior limbs covered with scalelike feathers, without remiges, and used as paddles when the birds are submerged; plumage covering the whole body. The horny sheath of the maxilla of from 3 to 5 pieces; schizognathous, without basipterygoid process; nares imperviae; bones of the anterior extremity strong, flattened; hallux without a web; metatarsals united at their extremities only; feathers with or without barbs, with aftershaft; with much subcutaneous fat; nests of grass or leaves in depression in the ground; two eggs, both sexes incubate; young blind; coasts of antarctic continent, southern temperate zone, one tropical species (Galapagos). *Aptenodytes patagonica* Forst., king-penguin (Fig. 252); *Spheniscus demersus* L., the Cape penguin; *Eudyptes chrysocome* L., Southern ocean, Falklands to New Zealand. Fossil forms from the Eocene of New Zealand (*Palaeudyptes*) and from the Miocene of Patagonia (*Paraptenodytes*, etc.).

\*Footnote on preceding page

Tribe 4. **PROCELLARIIFORMES (TUBINARES).** Petrels.

Ocean forms with great powers of flight, with webbed feet (palmate) and hallux absent or reduced to a stump. Horny sheath of the upper and lower beaks composed of several pieces; skull schizognathous; nostrils tubular. They usually select rocky and precipitous coasts for their breeding places. The female lays one egg and takes turn with the male in incubation. The young are nurtured for a long period. Cosmopolitan.

Fam. **Procellariidae.** With the characters of the tribe. About 100 species, more numerous in the S. hemisphere. *Procellaria pelagica* L., storm petrel or Mother Carey's chicken, Atlantic; *Diomedea exulans* L., wandering albatross, S. ocean; *Puffinus* Briss., Shearwater; *Daption* Steph., Cape pigeon; *Fulmarus glacialis* L., fulmar petrel; *Oceanites*, *Prion*.

Tribe 5. **CICONIIFORMES.**

Aquatic or marsh birds with wading feet. The vomer is complete, the palate desmognathous, without basipterygoid processes.

Fam. **Steganopodidae.** Large swimming birds with well-developed, often long and pointed, wings, and all the four toes united by a web. The newly-hatched young are blind and helpless and usually naked; known fossil since the Eocene. *Phaethon* L., tropic-bird, boatswain bird. *Sula* Briss., gannets and boobies, with subcutaneous extensions of the air-sacs, cosmopolitan except in the cold zones; *S. bassana* L., Solan goose. *Phalacrocorax* Briss., cormorants and shags; with many species (especially in New Zealand) cosmopolitan. *Plotus* L., Australia, Indo-Malaya, Air., C. and S. Amer.; *P. ankinga*, the snake-bird or darter. *Fregata* Cuv. (*Tacypetes* Vieill.), frigate-bird, tropical. *Pelecanus* L., pelicans, cosmopolitan except in cold zone.

Fam. **Ardeidae.** Herons, bitterns. Wading birds with long legs and neck; aquintocubital, with aftershaft; the young are long helpless. *Ardea* L., herons; *Botaurus* Steph., bitterns; *Nycticorax* Steph., night-heron; *Balaeniceps* Gould, shoebill; *Scopus* Briss., hammerhead.

Fam. **Ciconiidae.** Storks and ibis. The syrinx is without muscles; fossil from the Oligocene. *Ciconia* L., storks; *C. alba* L., Eur. to C. Afr., Asia. *Leptoptilus* Less., *L. crumenifer*, marabou stork, Afr.; *L. dubius*, the adjutant, India. *Tantalus*, *Abdimia*, *Mycteria*. *Eudocimus ruber* Vieill., the scarlet ibis of C. Amer.; *Ibis religiosa* Cuv., the sacred ibis of the Egyptians. *Platalea leucorodia* L., spoonbill.

Fam. **Phoenicopteridae.** Flamingos. With long legs and necks, beak



FIG. 252.—*Aptenodytes patagonica* (from Brehm).

bent down in the middle, covered with soft membrane, with horny lamellae at the sides, maxilla very moveable; hallux reduced or absent, toes fully webbed. Eocene to present. *Phoenicopterus* L., India, Afr., trop. Amer., S. Amer. *Palaelodus* M. Edw., extinct, Miocene.

#### Tribe 6. ANSERIFORMES.

Aquatic birds with desmognathous skull, basipterygoid processes, with two pairs of sterno-tracheal muscles, an evaginable penis, without or with rudimentary aftershaft. The beak is covered by a soft sensitive membrane and edged both above and below with horny lamellae. The young leave the nest early. From the Oligocene onwards.

Fam. **Palamedeidae**. Without uncinat processes and syrinx muscles. Pneumaticity very highly developed, air-cavities extending beneath the



FIG. 253.—*Chauna chavaria* (Règne animal).

skin and even into the fingers and toes. With two sharp spurs on the wings. *Chauna chavaria* Ill., the crested screamer or chajá (Fig. 253). Paraguay and Brazil, can be domesticated and used to herd flocks of fowls and geese in S. Amer. *Palamedea cornuta* L., the horned screamer.

Fam. **Anatidae**. Swans, geese, and ducks. Beak usually broad and depressed. The anterior toes usually fully webbed, hallux short and elevated. Neck unusually developed with extra vertebrae in the swans. Trachea often with elongations and dilatations especially in the male. Usually good flyers, but a few forms flightless (*Nesonetta*, *Tachyeres*). Good swimmers, frequenting either sea or fresh-waters. Cosmopolitan. About 150 living species. From the Eocene onwards. *Cygnus* L., swans

*C. olor* L., mute swan; *C. musicus* Bechst., whooper. *Anser* L., geese; *A. cinereus* Meyer, gray goose, origin of the domestic race; *A. hyperboreus* L., snow goose; *A. segetum* L., bean goose. *Cereopsis*, *Anseranas*, *Anas* L., ducks; *A. boscas* L., wild duck, origin of the domestic races. *Tadorna cornuta* Leach, sheld-drake. *Aex*, *Plectropterus*. *Fuligula*, *Somateria mollissima* Leach, eider duck; *Erismatura*. *Mergus merganser* L., goosander; *M. serrator* L., redbreasted merganser; *M. allellus* L. smew.

### Tribe 7. FALCONIFORMES.

Carnivorous birds with desmognathous skull, with curved beak hooked at the extremity, and with basal cere, without functional caeca. The feet are perching, and the strong toes are always armed with powerful claws which are admirably adapted for the seizure of prey which usually consists of warm-blooded animals. As a rule the female, which is larger than the male, alone incubates, but the male assists in procuring food for the helpless young. Fossil from the Eocene.

Fam. **Cathartidae**. With pervious nostrils and naked uropygial gland, without syrinx muscles, with complete basipterygoid processes. Western hemisphere. *Cathartes atratus* Baird, turkey-buzzard; *Catharista*, *Pseudogryphus*, *Gyparchus papa* Dum. the king-vulture; *Sarcorhamphus* Dum. *S. gryphus* Geoffr., the condor.

The remaining families of the tribe are grouped under the head *Accipitres*; with nares imperviae, feathered uropygial gland, and tracheo-bronchial muscles. The basipterygoid processes are not complete and the postacetabular part of the ilium is bent ventrally except in *Serpentariidae*.

Fam. **Serpentariidae**. The African secretary bird, *Serpentarius sagittarius* Cuv., feeds on insects and reptiles; with complete basipterygoid processes, about 4 ft. high, with long legs which easily break.

Fam. **Vulturidae**. Old-world vultures. Head and upper part of neck naked or with small down-like feathers. Old world from S. Central Europe to the Cape, absent from China, Malay Islands, Australia, Sumatra, Ceylon, Madagascar. *Vultur cinereus* Gm., S. Eur.; *Neophron percnopterus* Sav., Egyptian vulture. *Gyps fulvus* Briss., griffon; *Otogyps*, *Lophogyps*.

Fam. **Falconidae**. Head and neck feathered.

Sub-fam. **Gypaetinae**. *Gypaetus* Gray, cere feathered; *G. bartatus* Cuv., the lämmergeier, high mountains of Eur., Afr., Asia.

Sub-fam. **Polyborinae**. Carrion hawks. America. *Polyborus*, *Ibyster*, *Phalcobaenus*, *Senex*.

Sub-fam. **Accipitrinae**. Hawks. *Circus cyaneus* L., hen harrier; *C. cineraceus* Mont., Montagu's harrier; *C. aeruginosus* L., marsh harrier. *Astur palumbarius* L., goshawk. *Accipiter nisus* L., sparrow hawk.

Sub-fam. **Aquilinae**. Eagles. *Aquila chrysaëtus* L., golden eagle; *A. naevia* Briss., spotted eagle. *Haliaëtus albicilla* Briss., sea-eagle, erne.

Sub-fam. **Buteoninae**. Buzzards and kites. *Archibuteo lagopus* L., rough-legged buzzard. *Buteo vulgaris* L., buzzard; *Milvus iclinus (regalis)*, red kite, once common in London; *M. ater* Daud. black kite. *Pernis apivorus* Cuv., honey-buzzard.

Sub-fam. **Falconinae**. Falcons. *Falco gyrfalco* L., gyrfalcon;



*F. peregrinus* L., peregrine falcon; *F. aesalon* Tunst., merlin; *F. subbuteo* L., hobby; *F. tinnunculus* L., kestrel.

Fam. **Pandionidae**. Without aftershaft, with long feathered tibia; outer toe reversible. *Pandion haliaetus* Cuv., osprey or fish-hawk, nearly cosmopolitan.

#### Tribe 8. **TINAMIFORMES (CRYPTURI).**

Terrestrial birds with the power of strong and swift flight. The skull is dromaeognathous, the vomer being broad behind, fused with the palatines and interposed between the palatines, pterygoids and basisphenoidal rostrum. The quadrate articulates with the skull by a single facet. In this character, as well as in the posterior separation of the ischium and ilium, the absence of a pygostyle, they resemble Ratitae. The tail is abbreviated, usually with 10 weak rectrices, and the hallux is elevated. The tongue is small, there is a small penis; and the male takes part in the incubation. The eggs have a metallic gloss and the young are praecoces. They are confined to the Neotropical Region (extending into Mexico), with 30-40 species. Fossil forms are unknown. Their position is uncertain; by some zoologists they are placed with the Ratitae (see Pycraft, *op. cit.*).

Fam. **Tinamidae**. Tinamous, with principal genera, *Tinamus*, *Crypturus*, *Rhychotus* *Nothura*, *Eudromia*.

#### Tribe 9. **GALLIFORMES.**

Terrestrial or arboreal birds with a schizognathous skull, simple rhamphotheca, nares imperviae, and ten carpal remiges. They are quintocubital, and the feet are adapted for perching. They are good runners and seek their food on the ground, either in forests or in fields, feeding especially on berries, buds and seeds, and on insects and worms. They form rude nests usually on the surface of the ground or in low bushes, more rarely on high trees; and they lay a considerable number of eggs. Many are polygamous, but the male takes no part in building the nest or in the care of the brood. The young are for the most part praecoces. The hens are easily domesticated and, on account of their eggs and well-favoured flesh, have been made useful as domestic animals from the earliest times.

Fam. **Mesitidae**.\* With the single genus and species *Mesites variegatus* J. Geoffr. from Madagascar, to which it is confined. The bill is long and slender, the clavicles are absent, there are seventeen cervical vertebrae and 16 rectrices; there is no aftershaft. The condition of the young and the structure of the viscera are unknown.

Fam. **Turnicidae**. Quintocubital, with aftershaft, without hallux, with only left carotid. Small, solitary, non-migratory forms, which run quickly. The male incubates and feigns lameness. *Turnix* Bonn. (*Hemipodius* Reinw.) with about 9 species in S.-Eur., Africa, India.

Fam. **Pedionomidae**. Aqintocubital, with small hallux, with both carotids. *Pedionomus torquatus* Gould, Australia.

The three next families, *Megapodiidae*, *Cracidae*, and *Phasianidae* are grouped together as **Galli**.

\* This form is of very uncertain position. A. Milne-Edwards, who is the only man who has dissected it, placed it near the rails (*Ann. Sc. Nat.*, (6), 7).

Fam. **Megapodiidae**. Megapodes. The feet are large, the bill short, and the wings abbreviated. The eggs are placed in mounds or in holes in the sand, and develop without incubation. The young can fly almost immediately. Austro-Malayan, but not found in Borneo (?), Sumatra, or Java. *Megacephalon maleo* Temm., N. Celebes. *Megapodius tumulus* Gould, N.-E. of Australia. *Lipoa* Gould, S. Australia. *Talegallus*.

Fam. **Cracidae**. Curassows. Arboreal birds, with very pneumatic skeleton, feathered bursal glands and both carotids. Neotropical (except the Antilles). Several species are easily domesticated, but rarely breed in confinement. Hybrids with domestic fowls have been recorded. *Crax alector* L., curassow, S. Amer. *Penelope*, *Ortalis*, *Oreophasis*, etc.

Fam. **Phasianidae**. Essentially terrestrial birds, which, however, often roost in trees. Many polygamous, the male being larger and more brightly coloured than the female. The nests are placed on the ground, and the eggs are usually numerous. The head is usually adorned with coloured comb, cutaneous lobes or tufts of feathers. The hallux is elevated and usually without a claw, and the male frequently has spurs. They are mainly vegetable feeders, and nearly cosmopolitan in distribution. They are for the most part easily domesticated, and the breast muscles are well developed. From the Eocene onwards.

Sub-fam. 1. **Numidinae**. Guinea-fowls; Africa and Madagascar. *Numida meleagris* L., the guinea-fowl; W. Africa. *Acryllium*, *Guttera*, *Phasidus*.

Sub-fam. 2. **Meleagrinae**. Turkeys; N.-Amer., Central Amer.; *M. <sup>classica</sup> gallopavo* L., the origin of our farm-yard turkey, S. Canada to Mexico. *M. ocellata* Cuv., Honduras.

Sub-fam. 3. **Phasianinae**. Fowls. Inhabitants of the Old World. *Pavo cristatus* L., peacock, with long tail-coverts, India. *Argusianus giganteus* Tem., the argus-pheasant, Malay Penins., Sumatra. *Polyplectron* Tem., peacock-pheasant, Indo-China, Malaya. *Gallus* L., 4 species, India, Malaya; *G. ferrugineus* Gm. (*bankiva* Tem.), the red jungle-fowl and the origin of our domestic breeds, India, Malaya; *G. sonnerati* Tem., the grey jungle-fowl, India; *G. stanleyi* Gr., Ceylon; *G. varius* Shaw, Java. *Chrysolophus pictus* L., golden pheasant, China, E. Thibet. *Phasianus* L., pheasants, Eur., Asia; *Ph. colchicus* L., Caspian to S.-E. Eur., main origin of the introduced form, which has largely interbred with *Ph. torquatus* Tem., China, and *Ph. versicolor* of Japan, etc. *Catreus*, *Pucrasia*. *Gennaeus nycthemurus* L., silver-pheasant of S. China. *Crossoptilon*, *Lobiophasis*, *Lophura*, *Acomus*, *Lophophorus*, *Ceriornis*, *Ithaginis*.

Sub-fam. 4. **Tetraoninae**. Grouse, partridges, and quails. Nearly cosmopolitan except in S. Amer. *Ophrysia*, *Galloperdix*, *Synoeacus*. *Coturnix communis* Bonn., the common quail, Eur., Asia, Africa. *Perdix cinerea* Lath., the common partridge, Europe. *Francolinus*, *Caccabis rufa* L., the red-legged partridge. *Tetraogallus*, *Odontophorus*. *Bonasa sylvestris* L., hazel grouse. *Tympanuchus americanus* Reich., the prairie-hen. *Tetrao urogallus* L., capercally. *Lyrurus tetrix* L., black grouse. *Lagopus scoticus* Lath., red grouse, probably the insular form of the willow grouse, the only species of bird (except the St. Kilda wren) confined to the British Islands, not found south of Shropshire (except in S. Wales); *L. albus* Gm., willow grouse, becomes white in winter. *Colinus* and other genera (American "partridges").

Fam. **Opisthocomidae**.<sup>\*</sup> Fowl-like arboreal bird, without basipterygoid process; the anterior part of the keel of the sternum is aborted. Single genus and species *Opisthocomus cristatus* Gm., the hoazin, stink-bird, Guiana and Venezuela.

#### Tribe 10. GRUIFORMES.

Schizognathous, for the most part marsh birds, without basipterygoid process, with vomer, without crop, with an elevated hallux and a tracheo-bronchial syrinx. The nares are pervious in all except *Rhinocetus*. The young are covered with down.

Fam. **Rallidae**. Rails, coots, water-hens. Cosmopolitan, with about 150 species. The family includes some flightless forms in which the keel of the sternum is reduced. Most inhabit marshes or damp localities, but some (e.g. *Crex pratensis*) live on dry lands. The young are praecoces. Fossil from the Cretaceous onwards. *Rallus aquaticus* L., water-rail, N. and C. Eur. to C. Asia. *Crex pratensis* L., corncrake. *Pennula ecaudata* King, Sandwich Islands, flightless, extinct. *Gallinula chloropus* L., moorhen; *G. nesiotis* ScL., flightless, Tristan d'Acunha. *Fulica atra* L., coot, on the reedy lakes and ponds of Europe. *Himantornis* Tem., W. Africa; *Eulabeornis* Gould, Australia, Malaya, Madagascar, Polynesia. *Notornis*, *Aptornis*, flightless extinct birds from New Zealand; *Aphanapteryx*, Mauritius and *Erythromachus*, Rodriguez were probably extirpated by man. *Ocydromus* Wagl., the weka, New Zealand.

Fam. **Gruidae**. Cranes. Cosmopolitan except N. Zealand and Pacific Islands. Long-necked, long-legged waders. They have a powerful flight. The young are praecoces. *Grus cinerea* Bechst., the common crane of Eur. and N. Asia. *Balearica*, *Anthropoides*, *Aramus*.

Fam. **Psophiidae**. Trumpeters, trop. S. Amer.

Fam. **Cariamidae**. Sometimes placed with the secretary bird. *Cariama* Briss. (*Dicholophus* Ill.); *C. cristata* L., the seriema or crested screamer (a name also applied to *Chauna cristata*), Brazil, Paraguay; easily domesticated, will guard their owner's fowls.

Fam. **Otididae**. Bustards. Old World and Australia; about 25 species. *Otis tardus* L., great bustard, temp. Eur., and Russia to Persia, extinct as a native in England since 1838; *O. tetrax* L., little bustard, S. E. Eur.

Fam. **Rhinocetidae**. One genus and species, *Rhinocetus jubatus* Verr. and Des Murs, kagu, New Caledonia, with nares imperviae, somewhat larger than a fowl, and described as a generalised form.

Fam. **Eurypygidae**. With long neck, slender bill and pervious nostrils. One genus and two species: *Eurypyga helias* Pall., the sun-bittern, N.S.-Amer., *E. major* Hartl., Central Amer.

Fam. **Heliornithidae**. Finfoots. With small head, thin neck, toes with broad flaps and pointed claws, quintocubital, young are altrices, trop. S. Amer., Africa, Assam to Sumatra. *Heliornis*, *Podica*.

#### Tribe 11. CHARADRIIFORMES.

Terrestrial, arboreal, or marine birds with a schizognathous skull,

<sup>\*</sup> Of doubtful position. This family was placed by Huxley in a special group, *Heteromorphae*, and regarded by him as belonging to a more ancient type than the Galliformes (*Proc. Zool. Soc.*, 1868, p. 304; also Garrod, *Proc. Zool. Soc.* 1879, p. 109).

eleven primary remiges, a V-shaped furcula, and two carotids. They are aquintocubital. They fall into four groups, the *Limicolae*, the *Lari*, the *Pterocles* and the *Columbae*.

### Group 1. *Limicolae*.

The *Limicolae* are typically waders and good flyers. They are not, as a rule, habitual swimmers. The young are praecoces.

Fam. **Charadriidae**. Plovers, etc. They usually lay four spotted eggs. About 100 species; cosmopolitan.

Sub-fam. 1. **Charadriinae**. Premaxillary part of the beak hard. *Eudromias morinellus* L., the dotterel, Europe. *Charadrius pluvialis* L., the golden plover. *Aegialitis hiaticola* L., the ringed plover. *Anarhynchus frontalis* Q. and G., the wry-bill of N. Zealand. *Vanellus* L., lapwings; *V. cristatus* Mey., the lapwing, peewit or green plover.\* *Streptilas interpres* L., the turnstone. *Haematopus ostralegus* L., the oyster-catcher. *Himantopus* Barr., the stilts. *Recurvirostra avocetta* L., the avocet.

Sub-fam. 2. **Tringinae**. Premaxillary part of the beak soft and covered with a richly innervated skin; beak long, narrow, weak. *Phalaropus fulicarius* L., the grey phalarope. *Tringa alpina*, the dunlin. *Totanus calidris* L., the redshank; *T. (Actitis) hypoleucos* Temm., the sandpiper. *Machetes pugnax* Cuv., the ruff. *Limosa* Briss., the godwits. *Numenius arquata* L., the curlew.

Sub-fam. 3. **Scolopacinae**. The beak is long, and its premaxillary part is soft, covered by a richly innervated skin, and somewhat swollen. *Scolopax rusticula* L., the woodcock. *Gallinago caelestis* L., the common snipe; *G. gallinula* L., the jack snipe.

Fam. **Chionididae**. Sheathbills. Antarctic Seas.

Fam. **Glareolidae**. With *Glareola*, the pratincole; *Cursorius*, *Pluvianus*.

Fam. **Dromadidae**. *Dromas*.

Fam. **Thinocoridae**. With *Thinocorys*, *Attagis*.

Fam. **Oedicnemidae**. Without the hind toe. *Oedicnemus scolopax* Gm. (*crepitans* Tem.), the stone-curlew.

Fam. **Parridae**. Long-toed jacanas, with *Parra*, *Hydrophasianus*, etc.

### Group 2. *Lari*.

The *Lari* are typically swimmers and good flyers. The anterior toes have swimming membranes. Hallux small or absent. Mainly piscivorous. Young covered with down when hatched, but remaining for some time in the nest and fed by the parents.

Fam. **Laridae**. Wings long and pointed, praecoces. The sexes are similar.

Sub-fam. 1. **Larinae**. Gulls and skuas. Beak usually shorter than the head. About 50 species, cosmopolitan, mainly marine. *Stercorarius pomatorhinus*, the pomatorhine skua; *Megalestris catarractes* L., the great skua. *Rissa tridactyla* L., the kittiwake. *Larus* L., gulls.

\* Often served by cooks of a certain class as golden plovers. Diners who are unable to distinguish between the two by the coarser flavour of the lapwing, may do so by means of the sternum. In the golden plover there are two emarginations on each side of the posterior end of this bone; in the lapwing the inner of these is bridged so as to become a fenestration.



Sub-fam. 2. **Sterninae**. Terns or sea-swallows. Beak long, straight, tail usually forked. About 50 species, cosmopolitan. *Sterna hirundo* L., terns; *St. fluviatilis* Naum., common tern, coasts and inland waters of Europe, etc. *Gygis* Wagl. *Anous* Leach, noddies.

Sub-fam. 3. **Rhynchopinae**. *Rhynchops* L., skimmers, Indian Ocean and Atlantic side of Amer.

Fam. **Alcidae**. Auks. Piscivorous, marine, periarctic birds, with short wings (functionless in *Alca impennis*), heavy body, close plumage and fully webbed anterior toes. Most species fly strongly. Their common breeding places are on the coasts, where they lay their generally single egg on bare ledges of rock, in crevices, or in holes in the earth. *Alca impennis* L., great auk, flightless, extinct since 1844. *A. torda* L., razorbill. *Mormon arcticus* (*Fratercula* Temm.) Ill., puffin. *Uria troile* Lath., guillemot; *U. grylle* Cuv. black guillemot, tysty. *Mergalus alle* L., the little auk.

### Group 3. *Pterocles*.

Desert birds with short, feathered metatarsus; hallux small or absent; crop and caeca large. With nares imperviae, rudimentary vomer. The short front toes are enclosed in a casing which is covered as far as the claws with hairy plumage. Eggs three in number. The young are praecoces.

Fam. **Pteroclididae**. Sand-grouse. *Pterocles alchata* Gray, Eur., Africa, Asia. *Syrrhaptes paradoxus* Pall., Pallas' sand-grouse, Central Asia, occasionally wanders into and breeds in Europe.

### Group 4. *Columbae*.

The Columbae are most nearly allied to the *Pteroclididae*. They are of medium size, with small head, short neck, and short legs. The beak is longer than in the Galli, but weaker, and gently arched at the horny extremity. At the base of the beak the scaly cover of the nasal openings is swollen, naked and membranous. The rather long, pointed wings enable the bird to fly quickly and skilfully. The tail is weak and rounded, and contains usually 12, rarely 14, 16 or 20 rectrices. The plumage presents hardly any difference in the two sexes. The short legs are unfitted for rapid locomotion. The well-developed hind toe rests on the ground.

The vomer is small and often absent, and the nares impervious. The crop is paired and large, and at the breeding season secretes, in both sexes, a creamy fluid for the nourishment of the young.

There are about 350 species, distributed over all parts of the world. They live in pairs, or in flocks in forests, and feed mainly on grain and seeds. The species which live in the north are migratory; others make short migrations; while others are residents. They live in a state of monogamy, and lay two eggs (rarely one) in a rudely constructed nest. Both sexes take part in hatching and in bringing up the young, which are hatched almost naked ("pipers"), with closed eyelids, and, as altrices, require the care of the parents for a considerable time.

Fam. **Columbidae**. The beak with smooth edges, never dentated. *Columba livia* L., rock-pigeon (Fig. 254); slate-blue, with white wing covers and two black bands on the wings and the tail; is the ancestral form of the numerous races of domestic pigeon; nests on rocks and ruins, and is distributed from the coasts of the Mediterranean over a great part of



Europe and Asia. *C. aenas* L., the stock-dove; *Columba palumbus* L. the ring dove, wood pigeon. *Ectopistes migratorius* L., the passenger pigeon, N.-Amer. *Turtur auritus* Bp., the turtle-dove; *T. risorius* Sws. *Goura coronata* Flem., New Guinea. *Treron*, *Vinago*, *Carpophaga*, fruit-pigeons of tropical parts of the Old World; *Otidiphaps*, New Guinea.

Fam. **Didunculidae**. Beak compressed, lower jaw toothed, with hooked extremity. *Didunculus strigirostris* Gould, Samoan Islands.

Fam. **Dididae**. Large, extinct, flightless birds. Furcula and wings small, coracoid fused with scapula. *Didus ineptus* L., the dodo, Mauritius, found by the Dutch in 1598, and was last known as living in 1681. Several brought alive to Europe; pictures of these still exist; nearly complete skeletons in the museums of Cambridge, Paris, and Port Louis, one scarcely less so in the British Museum. It was an unwieldy bird, larger than a turkey, with lax plumage, powerful four-toed scraping feet, and strongly cleft beak. *D. borbonicus* Réunion, only known from travellers' descriptions. *Pezophaps solitarius* Gm., the solitaire, Rodriguez, was larger than a swan, extirpated about the same time as the dodo; two nearly complete skeletons in the Cambridge Museum, one scarcely less so in the British Museum.

## Tribe 12. CUCULIFORMES.

Arboreal birds with a desmognathous skull. The first and fourth toes are directed backwards (zygodactylous), but the fourth toe may be reversible. The young are altrices.

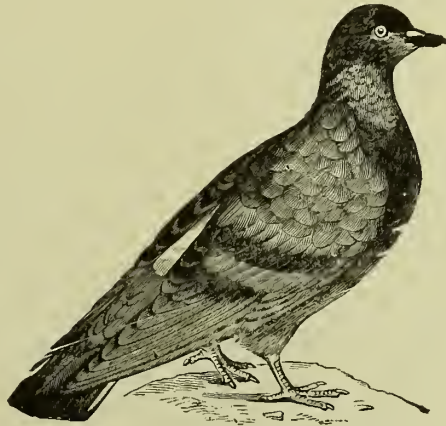


FIG. 254.—*Columba livia* (after Naumann).

### Group 1. *Cuculi*.

Quintocubital, zygodactylous arboreal birds. Cosmopolitan.

Fam. **Cuculidae**. Cuckoos. With gently-curved, deeply-cleft beak, long pointed wings, with ten primaries, and wedge-shaped pointed tail. The fourth toe can be directed forwards. About 200 species, cosmopolitan. *Cuculus canorus* L., the European cuckoo, adult somewhat like a sparrowhawk; it lays its eggs upon the ground and transfers them in its bill to the nests of other birds, usually of the meadow-pipit, the reed-warbler, the hedge-sparrow and the robin; the egg is incubated by its foster-mother and about 30 hours after hatching the young bird ejects the rightful young and eggs of the nest; the adults migrate to the South in July and August, but the young not till September or October, reaching as far as S. Africa, Ceylon, Celebes. The familiar cry is uttered by the male in the breeding season. They seem in some cases at least to use the nests of birds the eggs of which resemble their own. Other species of cuckoo have the same parasitic habit; e.g. *Coccyzus glandarius* L., the great spotted cuckoo of S. Europe. Other genera of cuckoos are *Chrysococcyx*, *Caco-*

*mantis* from the Old World, and *Saurothera*, *Diplopterus*, *Piaya*, *Coccyzus* from America; some of these are said to be parasitic, but most of them certainly build nests.

Other genera usually grouped under different sub-families are *Eudynamis*, *Phoenicophaea*, *Pyrhrocentor*, *Centropus*, *Coua*, *Geococcyx*, *Crotophaga*, *Guira*. Some of these build their own nests. In the case of *Crotophaga ani*, the black witch, several females unite to lay their eggs in a common nest.

**Fam. Musophagidae.** Touracos or plantain-eaters. About 20 species, at present confined to Africa. The fourth toe is reversible. The red feathers of the birds of this family owe their colour to a red pigment called turacin and containing 5 to 8 p.c. of copper and soluble in weak alkaline solutions. It is washed out by rain in the living bird, the feathers regaining their colour after an interval. A green pigment called turacoverdin is also found among these birds; it contains iron but no copper and is the only instance of a green pigment in the class. *Turacus* (*Corythaix*) *fischeri* of E. Afr.; *T. persa* L., W. Afr.; *Musophaga violacea* Isert, W. Afr.; *Schizorrhis* Wagl. *Necrorhis* fossil in the Miocene of France.

## Group 2. *Psittaci*.

Aquintocubital, zygodactylous, arboreal birds, with strongly bent beak, fleshy tongue and short metatarsus. The upper beak, which is covered at its base by a cere, is articulated with the frontal, and its long hooked extremity overlaps the short and broad lower beak. The parrots form a very sharply marked group, and the oldest known form, *Psittacus verreauxi* from the Lower Miocene of France, shows all the peculiar features of the group. Cosmopolitan, except in the colder regions; but their headquarters are Austro-Malaya; about 80 genera, and 500 species. The coloration is commonly gaudy. They are monogamous, but usually roost and feed in company.

**Fam. Trichoglossidae.** The tip of the tongue has fine horny fibres. *Nestor meridionalis* L., the kaka parrot of N. Zealand; *N. notabilis* Gould, the kea of the south island of N. Zealand, eats fruits, seeds and insects, but has lately acquired the habit of pecking holes with its powerful beak in the back and sides of sheep; there was a recently extinct species in Norfolk Island. The lorries form the bulk of this family, Austro-Malaya, Polynesia except N. Zealand; with principal genera, *Eos*, *Lorius*, *Trichoglossus*, *Oreopsittacus*. *Cyclopsittacus* also here.

**Fam. Psittacidae.** Parrots. With smooth tongue.

Sub-fam. 1. **Cacatuinae.** Cockatoos, Australian Region and Philippines; head with moveable crest, orbit complete, usually with only left carotid. *Calyptorhynchus*, *Cacatua*, etc. *Lophopsittacus mauritianus*, a contemporary of the dodo in Mauritius.

Sub-fam. 2. **Psittacinae.** Orbit and carotids vary, include the bulk of the parrots. *Melopsittacus undulatus* Shaw, the grass-parakeet or budgerigar, Australia. *Platycercus* Vig., Australia, N. Zealand, Society Islands. *Loriculus*, *Agapornis* Selby, Africa, *Psittacula* Ill., America, are the love-birds. *Palaeornis* Vig., Australia, Asia, Africa. *Psittacus erithacus* L., the grey parrot, the best talker, Africa. *Chrysotis* Sw. *Ara* Cuv., the macaws, Neotropical. *Nasiterna* Wagl., New Guinea and islands.

**Fam. Stringopidae.** Kakapo, of N. Zealand; with normal carotids, orbit

complete. *Stringops habroptilus* Gray, owl-like, with incomplete disc of feathers round the eye; a ground parrot which hides in holes in the daytime, with small power of flight; crista sterni hardly developed, clavicle dwindled to a mere spine united neither to its fellow nor to the sternum.

### Tribe 13. CORACIIFORMES.

Arboreal forms with short legs; they often nest in holes and have blind and helpless young. The tribe is difficult to characterize. It is divided into seven groups, the cross affinities of which with each other and with other tribes (Cuculiformes, Passeriformes, etc.) bring out clearly the impracticability of the so-called natural system of classification in linear or tree-like series.

#### Group 1. *Coraciæ*.

Fam. **Coraciidae**. Rollers. Beautifully coloured birds, with wide gape; beak with recurved extremity and sharp edges. With long wings and pedes fissi. *Leptosoma discolor* Herm., the kirombo, Madagascar and the Comoro Islands. *Coracias garrula* L., Eur., Afr., India. *Eurystomus* widely distributed; *Brachypteracias*, peculiar to Madagascar.

Fam. **Momotidae**. Motmots and todies. Neotropical, inhabiting forests. *Momotus*, *Todus*.

Fam. **Alcedinidae**. Kingfishers. With large head, long keeled angular beak, relatively short wings and tail; metatarsus short. *Alcedo ispida* L., kingfisher of Britain and Europe. *Alcyon* Sw., Austro-Malaya. *Dacelo gigas* Glog., the laughing jackass of Australia. *Ceyx*, *Halcyon*, *Tanyptera*. *Ceryle rudis* L., black and white kingfisher, Africa.

Fam. **Meropidae**. Bee-eaters. The beak is compressed and gently curved downwards. The plumage is variegated, the legs are weak. The wings are pointed, with long coverts. The flight is rapid and swallowlike. Temperate and tropical parts of the Old World, about 30 species. *Merops apiaster* L., S. Europe. *Nyctiornis*, *Melittophagus*.

Fam. **Upupidae**. Hoopoes. Beautifully coloured birds with long laterally-compressed beak, short triangular tongue, and long rounded wings. About 65 species; Old World except Australia. *Upupa epops* L., Europe, Africa, Asia. *Irrisor*, *Rhinopomastus*.

Fam. **Bucerotidae**. Hornbills. Birds of considerable size, with colossal, always slightly dentated, and downwardly-curved beak and usually with hornlike head-dress at the base of the upper beak. Bones very pneumatic. Ethiopian and Indo-Malayan. *Bucorvus abyssinicus* Gm. *Bucerus rhinoceros* L., Sumatra. *Rhinoplax*, *Aceros*, *Lophoceros*, *Anorhinus*, etc.

#### Group 2. *Striges*.

With single Fam. **Strigidae**. Owls. Nocturnal birds of prey which hunt insects and small mammals, birds, reptiles, etc. With large anteriorly directed eyes which are surrounded by a circle of stiff feathers, sometimes in a veil-like manner; with strong hooked beak, bent downwards from the base. The ear usually has a membranous operculum and external cutaneous fold, on which the feathers may be grouped so as to give the appearance of a pinna. Cosmopolitan, about 150 species. Fossil from the Eocene. *Strix flammea* L., screech, or barn, owl (Fig. 255), cosmo-

politan. *Syrnium aluco* L., the tawny or wood owl, Britain except Ireland, Africa, Asia. *Asio otus*, long-eared owl, Europe, Asia, etc.; *A. brachyotus* Gm., short-eared owl. *Bubo ignavus*, eagle owl, Eur., Asia, N. Afr. *Nyctea nivea* Daud. (*scandiaca* L.), snowy owl, a diurnal owl. *Surnia*, *Scops*, *Sceloglaux*, *Carine*.

### Group 3. *Caprimulgi*.

Nocturnal, wide-mouthed birds, owl-like in appearance.

Fam. 1. **Caprimulgidae**. Night-jars or goatsuckers. Cosmopolitan with about 80 species and several genera. Their size varies from that of a lark to that of a crow. The plumage is soft, owl-like, mottled and pencilled with grey, chestnut, brown, black and white. The beak is short, flat, and triangular, gape enormously wide and often beset with stiff bristles. The legs are weak and short. Hind toes reversible; outer toe with 4 phalanges only, a most unusual character among birds; middle toe long and sometimes with a serrated claw. They live for the most part in forests and feed especially on moths, which they catch during flight. As a rule they lay two eggs on the

bare ground, without even scraping a hole for their reception. *Caprimulgus* L., the buccal slit extends to close behind the eyes; edge of beak not dentated, fringed with stiff bristles; cosmopolitan. *C. europaeus* L., night-jar, goat-sucker, or fern-owl, Britain, Eur., Afr., Asia.

*C. ruficollis* Temm., Spain. *Nyctibius*, *Macrodipteryx*, *Hydropsalis*, etc.

Fam. **Podargidae**, Australia, Papuaasia, Indo-Malaya, with *Podargus*, *Batrochostomus*, *Aegotheles*.

Fam. **Steatornithidae**. With the single genus and species *Steatornis caripensis* Humb., the guacharo or oil-bird, in mountainous country from Trinidad to

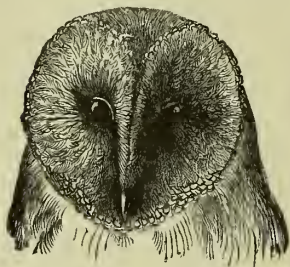


FIG. 255.—Head of *Strix flammea*.

Peru, lives on fruit or oily nuts.

### Group 4. *Cypseli*.

Swifts and humming-birds, with long wings and deep-keeled sternum, without intestinal caeca.

Fam. **Cypselidae**. Swifts. Swallow-like, with narrow wings forming an almost continuous curve when extended, short feathered metatarsus and strongly-clawed feet (*p. adhamantes*), sometimes with inwardly directed hallux. In *Cypselus* and *Panyptila* the digital formula is unique, being 2, 3, 3, 3. There are 10 rectrices and 10 secondary remiges. Cosmopolitan, except in N. Zealand and the cold zones; about six genera and 80 species. They are extraordinarily strong flyers, and they spend a great part of their time on the wing, catching the insects which form their food. They are remarkable for the development of their salivary glands, the secretion of which is of a glutinous character and serves to glue together the materials of which the nest is composed. In the genus *Collocalia* the nest is entirely formed of this secretion (the edible nest used by Chinese epicures for making soup). The nest is sometimes of remarkable architecture. *Cypselus apus* L., the common swift; *C. melba* L., the alpine



swift. *Panyptila* Cab., America. *Collocalia* G. R. Gr., India and Australia, chiefly the islands of the Indian Ocean; they breed in company and make their nests in caves or on the surface or bare face of a cliff. *Macropteryx*, *Acanthyllis* Ag. (*Chaetura*), with the shaft of the rectrices projecting in spines.

Fam. **Trochilidae**. Humming-birds. Among them are the smallest of birds. The plumage is variegated with a metallic lustre. The beak is long and awl-shaped, and the long tongue which is cleft to the root can be projected in the form of a double tube. There are 10 primary remiges and 10 rectrices. They are insectivorous, spending most of their time flitting from flower to flower in which they find their food. Confined to America and West Indies; 400 to 500 species. *Rhamphodon naevius* Less., Brazil. *Phaethornis superciliosus* Sw., Brazil. *Trochilus colubris* L. *Lophornis magnifica* Pp., Brazil. *Loddigesia mirabilis* Gould, Peru. *Patagona gigas*, the largest of the group,  $8\frac{1}{2}$  inches long, Patagonia; *Mellisuga minima*, the smallest  $2\frac{3}{8}$  inch, Jamaica.

#### Group 5. *Colii*.

This group includes the single family **Coliidae**, called the mouse-birds either from their creeping habits or from their colour. The hallux is reversible, but commonly directed forwards. They are small frugivorous forest birds with long tail and short dense plumage and are confined to Africa; about 9 species, *Colius* Briss.

#### Group 6. *Trogones*.

With the single family **Trogonidae**. The only heterodactylous birds, i.e. the first and second toes are directed backwards, the third and fourth forwards. Tropical, usually brightly-coloured, insectivorous and frugivorous forest birds. The skull is schizognathous; the beak is short and strong, usually with serrated edges; the mouth is wide with bristles at the corners. There are 10 primaries and 12 rectrices. About 40 species; Central and South America, Africa, and Indo-Malaya. *Trogon curucui* L., Brazil. *Pharomacrus mocinno* de la Llave, the quesal, Vera Paz and Guatemala. *Haploderma* Ag., Africa. *Harpactes* Sw., Indo-Malaya. *Trogon gallicus* M. Edw., from the Miocene of France.

#### Group 7. *Pici*.

Zygodaetylous birds, i.e. 1st and 4th toes directed backwards, the other toes forward with a variable palate (schizognathous, aegithognathous, or desmognathous).

Fam. **Galbulidae**. Jacamars. Desmognathous, with large precoracoid process, functional caeca and normal carotids, 10 primaries, and 10 or 12 rectrices. Confined to Central and tropical South America. *Galbula* Moehr., jacamars. *Jacamarhalyon*, ~~*Picoides*~~, *Urogalba*. *Bucco*, L., puff-birds.

Fam. **Capitonidae**. Aegithognathous, without caeca, with left carotid only.

Sub-fam. 1. **Capitoninae**. Barbets. Asia, Ethiopian, Neotropical, about 100 species in tropical forests. With brilliant plumage. *Capito*, *Cyanops*, *Barbatula*, *Gymnobucco*, *Megalaema*, *Pogonorhynchus*.



Sub-fam. 2. **Indicatorinae**. Honeyguides. About 12 species, Ethiopian and Indo-Malayan. They conduct travellers to bees' nests, their object being to get the young bees. *Indicator*, *Protodiscus*.

Fam. **Rhamphastidae**. Toucans. Extraordinary birds with huge but quite light bills, marginally serrated beak and horny, brushlike non-protractile tongue. About 50 species in the tropical forests of Central and South America. *Rhamphastus toco* L. *Pteroglossus aracari* Ill. *Selenidera*, *Aulacorhamphus*.

Fam. **Picidae**. Woodpeckers. Powerfully built birds, with schizognathous palate, strong chisel-shaped beak pointed in front, without cere. Metatarsus with transverse scales, feet with strong claws, with hard, firm tail used as a prop in climbing trees. The tongue is long, flat, and horny, and bears at its end short recurved hooks; it can be rapidly protruded to a considerable distance in consequence of a peculiar mechanism of the hyoid bone. The cornua of the hyoid are bent into wide arches and in some extend over the skull to the base of the beak. There are about 350 species found in all temperate and tropical lands except Madagascar, Australia, and Polynesia.

Sub-fam. 1. **Picinae**. Woodpeckers. For the most part solitary woodland birds of a shy and retiring nature, with powerful chisel-like beak and very extensile tongue. They bore holes in trees, in which they lay their eggs. *Picus martius* L., black woodpecker, Europe and Asia, not in Britain. *Dendrocopus major* L., the greater spotted, and *Dendrocopus minor*, the lesser spotted woodpecker, both British, also in Europe and N. Asia. *Gecinus viridis*, the green woodpecker, British, also in Europe and N. Asia. There are about 50 genera, of which we may mention, *Melanerpes*, *Picoides* (with 3 toes only), *Meiglyptes*, *Tigan*, *Picumnus*, *Sasia*.

Sub-fam. 2. **Iynginae**. Wrynecks, with one genus *Iynx* L., Europe, Asia, Africa, with soft tail and naked nostril and extensile tongue. They feed chiefly on the ground and utilise ready-made cavities for their eggs. *I. torquilla* L., wryneck, British.

#### Tribe 14. **PASSERIFORMES**.

The passerine birds are quintocubital; the palate is aegithognathous, without basipterygoid process, generally with large backwardly directed processes of the palatines; hallux invariably large and backwardly directed; front of shank covered with a small number of large scales; left carotid only present. The caeca are small, and the young are altrices. The number of species is enormous, about 5,500 or more than half the total number of living birds, but the variation in structure is very small, and the families have not the value even of those of the other tribes of birds. The families are grouped according to the arrangement of the muscles of the syrinx.

##### Group 1. *Passeres Anisomyodae (Clamatores)*.

The syrinx muscles are either entirely lateral, or only dorsal or only ventral.

Fam. **Eurylaemidae**. Broad-bills, Indo-Malaya; 10 species. *Eurylaemus*, *Psarisomus*, *Calyptomena*.

Fam. **Pittidae**. Tropics of the Old World, about 50 species. *Pitta*, Afr., Ind., Aust. *Philepitta*, Madagascar.

Fam. **Xenicidae**. New Zealand, 3 species. *Xenicus*.

Fam. **Tyrannidae**. America. Over 400 species. *Tyrannus carolinensis* Gm., the king or tyrant bird, temp. N. Amer. *Oxyrhamphus*.

Fam. **Pipridae**. Trop. Amer. *Pipra* Bonn., manakins, S. Amer.; *Tityra*.

Fam. **Cotingidae**. Trop. Amer. *Cotinga*; *Rupicola*, cock of the rock; *Gymnoderus*, *Coracina*, etc.

Fam. **Formicariidae**. South and Central America. Some are schizognathous, and some have lost the tracheo-bronchial muscles. About 520 species *Thamnophilus*, *Formicarius*, *Grallaria*, *Furnarius*, *Dendrocolaptes* etc.

Fam. **Pterotochidae**. South America; about 30 species. *Pterotochus*, *Hylactes*, *Conopophaga*.

#### Group 2. *Passeres Diacromyodae (Oscines)*.

The syrinx muscles are inserted both on the dorsal and on the ventral ends of the bronchial rings.

##### A. *Abnormales, Suboscines*.

Fam. **Menuridae**. Lyre-birds. Large birds with a stout beak. With 11 primaries and 16 rectrices of which the two outer are curved like a lyre in the male. Incompletely aegithognathous. They live in forests with tangled undergrowth, and are good mimics. *M. <sup>menura</sup>superba* Dav.

Fam. **Atrichornithidae**. Scrub-birds. Australia. Small birds inhabiting dense scrub or grassy lands; good mimics. Australia. *Atrichornis*.

##### B. *Normales, Oscines verae*.

Fam. **Alaudidae**. Larks. The plumage is earth-coloured; the beak is of medium length, the wings broad and long and the tail short. *Alauda arvensis* F., skylark; *A. arborea* L., woodlark; *A. cristata* L., crested lark; *A. alpestris* L., shore lark.

Fam. **Motacillidae**. Wagtails and pipits. Body slender; beak fairly long and notched at the point. *Anthus pratensis* Bechst., meadow pipit *Motacilla alba* L., white wagtail.

Fam. **Henicuridae**. Fork-tails.

Fam. **Timeliidae**.

Fam. **Pycnonotidae**. Bulbuls.

Fam. **Muscicapidae**. Flycatchers. Beak short, broad, and depressed at the base, somewhat compressed anteriorly, with hooked curved point. *Muscicapa grisola* L., *M. atricapilla* L.

Fam. **Turdidae**. Thrushes, warblers, etc. The beak is tolerably long, somewhat compressed, slightly notched before the point, and furnished with vibrissae at the base. The metatarsus is long, and covered with an anterior and two lateral scales (laminipantar). *Turdus merula* L., blackbird; *T. viscivorus* L., mistletoe thrush; *T. musicus* L., thrush; *T. torquatus* L., ring-ousel; *T. iliacus* L., redwing; *T. pilaris* L., fieldfare; *T. migratorius* L., American robin; *T. (Monticola) saxatilis* L., rock-thrush; *T. cyanus* L., blue thrush. *Saxicola* Bechst., wheatear. *Praticola rubetra*, L., whinchat; *P. rubicola* L., stonechat. *Ruticilla phoenicurus* L., redstart. *Accentor modularis* L., hedge-sparrow. *Luscinia philomela* Bechst., thrush nightingale, large nightingale in E. Europe; *L. luscinia* L., nightingale; *L. (Erithacus) rubecula* L., robin redbreast.

Fam. **Cinclidae**. Dippers or water-ousels. *Cinclus aquaticus* Bechst.

Fam. **Troglodytidae**. Wrens, principally in trop. America. *Troglodytes parvulus* Koch, the common wren.

Fam. **Chamaeidae**. One genus, N. Amer.

Fam. **Hirundinidae**. Swallows and martins. With 12 rectrices and anteriorly scutellated metatarsus. With broad, triangular beak, split nearly to the eyes. Feet small and weak. Tail long and forked. Cosmopolitan; the European species pass the winter in Central Africa. The nests are formed of small lumps of moist earth and short straws and slender sticks. *Hirundo rustica* L., the swallow. *Chelidon urbica* L., the house-martin. *Cotile riparia* L., the sand-martin, nests in holes in the earth, which it digs for itself.

Fam. **Campephagidae**. Cuckoo-shrikes. *Orynotus* of Mauritius and

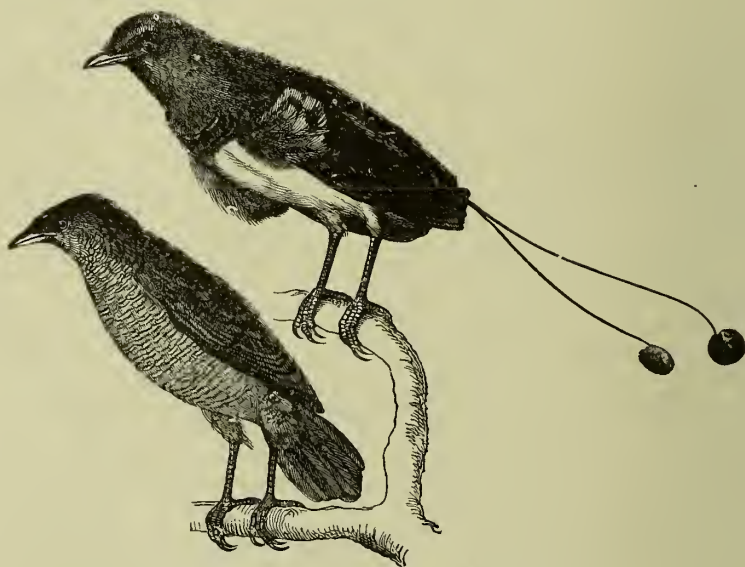


FIG. 256.—*Cincinnurus regius*, male and female (from Claus).

Réunion has two species in which the males are alike, the females being very different.

Fam. **Dicururidae**. Drongos. Ethiopian, Indian and Australian Regions.

Fam. **Ampelidae**. *Ampelis garrulus* L., the waxwing, Arctic Europe, Asia and America; *A. carolinensis*, cedar bird of N. Amer., *A. japonicus* Japan and Amuria.

Fam. **Artamidae**. Wood-swallows, from the Australian to the Indian Regions.

Fam. **Laniidae**. Butcher-birds or shrikes. Large powerful passerines, with hooked, strongly serrated beak, strong rictal vibrissae, and tolerably long, sharply clawed, feet. *Lanius excubitor* L., grey shrike; *L. minor* L., lesser grey shrike; *L. rufus* L., woodchat shrike; *L. collurio* L., red-backed shrike. These birds prey on small mammals, birds, etc., and impale them on thorns to be devoured at leisure.

Fam. **Vireonidae**. Greenlets, America.

Fam. **Sittidae**. Nuthatches. *Sitta caesia* W. & M., the British species of nuthatch.

Fam. **Paridae**. Tits. Small, beautifully coloured and agile birds of stout build, with sharp, short, almost conical beak. *Parus major* L., great titmouse; *P. ater* L., coal titmouse; *P. caeruleus* L., blue titmouse; *P. cristatus* L., crested titmouse; *P. palustris* L., marsh titmouse; *P. caudatus* L., long-tailed titmouse. *Aegithalus pendulinus* L., penduline titmouse.

Fam. **Oriolidae**. Old-World orioles. Palaearctic, Oriental and Australian Regions. *Oriolus galbula*, the golden oriole, Europe.

Fam. **Paradisidae**. Birds of Paradise; Australian Region. With slightly curved, compressed beak, large toes, and strong feet. The males are gorgeously attired, with tufts of lax feathers at the sides of the body and on the neck and breast. The two middle rectrices are often elongated and filiform, with small vane only at the extremity. *Paradisaea apoda* L. *Cincinnurus regius* L., New Guinea (Fig. 256). *Pteridophora alberti*, New Guinea.

The **bower-birds** of Australia (*Ptilorhynchus*, *Chlamydera*, *Sericulus*, *Amblyornis*, *Prionodura*, etc.) are placed here. They construct "runs" or "playing houses" with pieces of sticks and grass, and in some cases ornament them with mosses, flowers, feathers, shells, etc. It is not clear whether the bowers are constructed by birds of both sexes or by the males only.

Fam. **Corvidae**. Beak strong and thick, somewhat curved anteriorly and slightly notched. *Corvus corax* L., raven; *C. cornix* L., hooded crow; *C. corone* L., carrion crow; *C. frugilegus* L., rook; *C. monedula* L., jackdaw. *Pica caudata*, magpie; *Garrulus glandularius* L., jay. *Nucifraga caryocatactes* L., nutcracker. *Pyrrhocorax* V., choughs.

Fam. **Sturnidae**. Starlings. With straight or slightly curved, strong beak, the point of which is rarely only slightly notched; without rictal vibrissae. Old World, not America. *Sturnus vulgaris* L., starling. *Pastor roseus* Temm., rose-coloured starling. *Buphaga africana* L., ox-pecker.

Fam. **Drepanididae**. Sandwich Islands.

Fam. **Meliphagidae**. Honey-eaters. Australian Region. Small beautifully-coloured birds of stout build, with muscular vocal apparatus, long gently-curved beak, wings of medium length and long tail. *Meliphaga auricomis* Sw.

Fam. **Zosteropidae**. White-eyes. Ethiopian, Indian, Australian Regions.

Fam. **Nectariniidae**. Sun-birds. With brilliant metallic coloration. India, Papuasia, N. Australia, Africa. *Nectarina splendida* Cuv., S. Africa.

Fam. **Dicaeidae**. Flower-peckers. India, Australia, W. Africa.

Fam. **Certhiidae**. Creepers. With long slightly-curved beak, horny tongue, and long hind toe with sharp claw. Palaearctic, Nearctic, Ethiopian, Australian Regions. *Certhia familiaris* L., common creeper. *Tichodroma muraria* Ill., wall-creeper.

Fam. **Coerebidae**. Quitquits. America.

Fam. **Mniotiltidae**. American warblers.

Fam. **Tanagridae**. America.

Fam. **Ploceidae**. Weaver-birds. So called from the elaborately woven

nests which many of them build. Ethiopian, Indian, and Australian Regions ; about 250 species.

Fam. **Icteridae**. American orioles or starlings.

Fam. **Fringillidae**. Finches. With short thick swollen beak, without notch, with a basal swelling. *Emberiza citrinella* L., yellow bunting ; *E. cia* L., meadow bunting ; *E. nivalis* L., snow bunting. *Fringilla coelebs* L., chaffinch ; *F. spinus* L., siskin ; *F. montifringilla*, brambling ; *F. carduelis* L., goldfinch. *Passer domesticus* L., house-sparrow ; *P. montanus* L., tree-sparrow. *Coccothraustes vulgaris* Pall., hawfinch. *Pyrrhula vulgaris* Briss., bullfinch ; *P. canaria* L., canary. *Loxia curvirostra* Gm., crossbill. *Linota cannabina*, linnet.



## CHAPTER XIII.

### CLASS MAMMALIA.\*

*Warm-blooded hairy animals with double occipital condyle, a heart with two ventricles and two auricles, a left aortic arch, non-nucleated red blood-corpuscles, and mammary glands with which they suckle their young. The lower jaw consists of a single piece on each side and articulates with the squamosal, and the ureters always (except in Monotremeuta) open into the bladder.*

In addition to the characters mentioned in the definition which absolutely characterise the Mammalia, we may mention the following which are almost universally present.

The external auditory meatus is tubular and its opening is almost always marked by a fold of skin called the *pinnu*. There are three ossicles, the malleus, incus and stapes, connecting the tympanic membrane with the fenestra ovalis. The cochlea is spirally coiled. The retina contains blood-vessels. The tym-

\* J. C. D. v. Schreber, *Die Säugethiere in Abbildungen nach der Natur mit Beschreibungen*, fortgesetzt von J. A. Wagner, 1-7, and sup. 1-5, Leipzig 1775-1855. E. Geoffroy St. Hilaire et F. Cuvier, *Histoire Naturelle des Mammifères*, Paris 1840-45. A. E. Brehm., *Illustriertes Thierleben*, 1-3. De Blainville, *Osteographie*, 1835-54. Huxley, *Anatomy of the Vertebrata*, London, 1871. Flower, *Osteology of the Mammalia*, 3rd ed. 1885. Flower & Lydekker, *Mammals living and extinct*, London, 1891. Beddard, *Mammalia*, vol. 10 of the Cambridge Natural History, 1902. R. Owen, *Odon-tography*, 2 vols., London, 1840-45. Tomes, *Dental Anatomy*, 5th ed., London, 1898. Wallace, *Geographical Distribution of Mammals*, 2 vols. London, 1876, and *Island Life*, London, 1880. W. L. & P. L. Selater, *The Geography of Mammals*, London, 1899. Lydekker, *Geographical History of Mammals*, Cambridge, 1896. Trouessart, *Catalogus Mammalium tam viventium quam fossilium*, Berlin, 1897. Zittel, *Handbuch der Palaeontologie*, vol. 4, Leipzig, 1891-3, and *Grundzüge der Palaeontologie*, Leipzig, 1895. Woodward, *Outlines of Vertebrate Palaeontologie*, Cambridge, 1898. F. M. Balfour, *A Treatise on Comparative Embryology*, vol. 2, London, 1882. C. S. Minot, *Human Embryology*, New York, 1892. A. M. Marshall, *Vertebrate Embryology*, London, 1893.

panic cavity is bounded ventrally by a tympanic bone, and the quadrate is not present as a distinct element being probably absorbed into the squamosal. There is no postfrontal bone and only one temporal arcade (see p. 319). The vertebral centra almost always carry epiphyses. There are almost always seven cervical vertebrae. The coracoid is with one exception reduced, and fused with the scapula, not reaching the sternum. Except in whales, the pollex and hallux usually have two phalanges, the other digits three. When the digits are reduced the order of disappearance is almost always No. 1, No. 5, No. 2, No. 4, so that if there is only one digit it is No. 3, if two Nos. 3 and 4. In the brain the cerebellum has two lateral lobes as well as a median, there are four optic lobes (*corpora quadrigemina*), and the cerebral hemispheres are connected by a broad commissure, the *corpus callosum*. The portions of the body cavity containing the lungs are always separated from the general body cavity by a muscular septum, the *midriff* or *diaphragm*. There is a urogenital sinus, called urethra in the male and vestibule in the female, which receives the opening of the bladder and of the generative ducts; it opens independently of and ventral to the anus except in the Monotremata and a few other forms.

The testes and ovaries have nearly always shifted backwards in the body cavity from their primitive position near the kidney; in the case of the male the shifting is considerable and the testes very generally lie in pouches of the body cavity called the scrotal sacs, placed close to the root of the penis. A penis is always present, consisting of two corpora cavernosa attached to the ischia and of a corpus spongiosum which swells terminally to form the glans penis. With very rare exceptions the penis is traversed by the urethral canal. The female has a reduced homologue of the penis, the *clitoris*, which is only rarely traversed by the urethra.

In addition to the peculiarities in the vascular system mentioned in the definition, viz. the four-chambered heart and the presence of an aortic arch on the left side only, it ought to be mentioned that there is no renal-portal circulation.

The ovum is always small and provided with but little food yolk. As might be expected the cleavage is total and the greater part of the development (excepting in the Monotremata in which the cleavage is partial) takes place in that portion of the oviduct,

to which the term *uterus* is applied. The embryo is provided with an amnion and allantois and, excepting in the Monotremata and most Marsupialia, is always connected with the uterine wall by means of the allantois; the combined structure formed by the union of foetal and maternal tissues being called the *placenta*.

Such are the principal characters of the Mammalia. It will be seen that the group is a very well defined one and clearly marked off from the other vertebrate classes. As to its origin in evolution we have nothing to say for the very good reason that there are no facts by which we can arrive at any conclusion on the subject. It may however be noted here that, if we except certain doubtful forms from the Eocene, the Monotremata are not found fossil till the Pleistocene, and that the earliest known fossil mammals appear, so far as can be judged from their somewhat scanty remains, to have been of a small and rather specialised type. It is true that these Triassic and Jurassic Mammalia are classified with or in the neighbourhood of the Marsupialia, but it cannot be asserted that this is done on any substantial evidence.

But we may say something with regard to the relations of Mammalia to other classes of Vertebrata. Though a well defined group they present rather close points of contact with living reptiles through the Monotremata (p. 525) and especially with the extinct Anomodontia (p. 398). The resemblances between Monotremata and living reptiles are specially interesting because they concern the soft (urinogenital organs, ovum, etc.) as well as the hard parts (shoulder girdle, etc.). Taking the totality of these resemblances they reduce the important features of soft parts which are peculiar to mammals to the red blood-corpuscles, the aortic arch, the mammary glands and the hairs. Treating the skeleton in the same way, we find that, having regard to the Anomodontia and the Monotremata there is hardly a character of any importance which can be said to be peculiar to Mammalia. We thus reach the conclusion that the gap between reptiles and mammals is not a large one, that it is not indeed larger than that between reptiles and birds, and that reptiles, birds, and mammals constitute a natural group, more homogeneous than the group Ichthyopsida or even than the class Pisces. Among the characters of the group so constituted we

may mention the terrestrial habit and the absence of gills, the presence of an amnion and allantois, the universal presence and relative importance of the hyomandibular cleft, the presence of a primitive streak, of twelve pairs of cranial nerves, the absorption of the persistent part of the mesonephros into the testis, the presence of a ureter, the abortion in the adult female of the mesonephric duct, and lastly the complete disappearance of the conus arteriosus and the breaking up of the ventral aorta.

By these important characters the reptiles, birds, and mammals

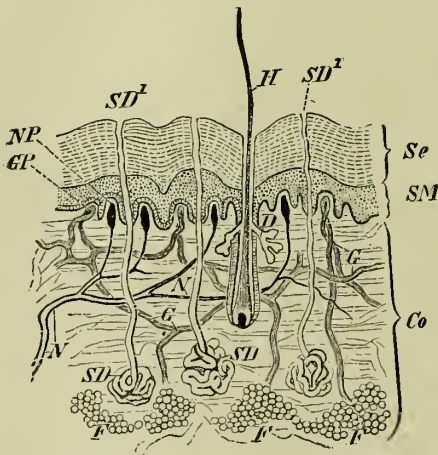


FIG. 257.—Section of human skin (from Wiedersheim. *Co* dermis (*corium, cutis*); *D* sebaceous glands; *F* subcutaneous fat; *G* bloodvessels of dermis; *GP* vascular papilla of hair; *H* hair; *N* nerves in dermis; *NP*, nerve ending in dermis; *Se* horny layer of epidermis (*stratum corneum*), *SD* sweat gland; *SD'* duct of sweat gland; *SM* malpighian layer of epidermis (*stratum malpighii*).



are sharply marked off from both Amphibia and Pisces; the more we consider them, the more difficult it becomes to understand on what grounds the contention has been made that mammals are more closely related to Amphibia than to reptiles and have been directly derived from them in evolution.

We shall now proceed to give some account of such features of mammalian anatomy as seem to require a fuller explanation

to enable the reader to comprehend the detailed descriptions of the orders which follow. Space does not permit of our giving anything like a complete account of mammalian morphology. For such we must refer the reader to special works on Anatomy and Embryology.

Hairs are to mammals what feathers are to birds. They are never entirely absent; even Cetacea and the hippopotamus which seem to be without them, possess hairs on certain parts even if only a few short bristles on the lips. Hairs are cornified modifications of the epidermis. The bulbous root is placed

upon a vascular papilla at the bottom of an epidermal pit (hair-follicle) which projects into the dermis some distance below the level of the epidermis (Fig. 257); the upper part or shaft projects freely on the surface of the skin. Each hair is composed of an axial part—the *pith*, which contains air, and of an outer horny part—the *cortex*, in which there is no air. The cortical part is frequently imbricated so as to appear scaly, e.g. bats; in the sloths it is fluted longitudinally. In some cases the pith predominates, while in others, as in bristles, the horny cortical part is the more important. Two kinds of hairs may be distinguished according to the nature of the shaft; contour hairs which are stronger and longer, and woolly hairs which are delicate and curled and surround the base of the contour hairs. The woolly hairs constitute the under-fur; they frequently have the power of cohering (felting) by their rough scaly surface. Hairs are usually cylindrical, but sometimes they are flattened; in the latter case they tend to curl. In some animals the hair is renewed periodically, and in some the hair in winter is longer than and of a different colour from the hair of summer. Smooth muscular fibres are often attached to the sheaths of the stronger hairs, by means of which each of them can be moved singly. The bristling of the hairy covering and the erection of the spines over larger extents of surface is caused by the striped muscular system of the dermis. Horny epidermal scales are found in some Edentates (*Manis*), and occasionally on the under surface of the tails of rodents. The horny scales of armadillos are placed over bony dermal plates. Special cornification of the epidermis is also found over the terminal phalanges of the digits in the form of nails, claws, and hoofs.

**Cutaneous glands.** Sweat glands  and  sebaceous glands (Fig. 257) are widely distributed. Sebaceous glands are almost invariably found opening into the hair-follicle, but they are also found on naked parts of the skin. They secrete a fatty grease which keeps the surface soft and the hair glossy. Sweat glands have the form of coiled glandular tubes with sinuous ducts, and are rarely absent (*Cetecea*, *Mus*, *Talpa*). The larger glands with strongly smelling secretions, which open on various parts of the integument of many mammals are to be regarded as modified sebaceous, or more rarely sweat-glands. As examples of such glands may be mentioned the occipital glands of the camel, the



glands (*crumen*) which are placed in a depression of the lacrymal bone of antelopes and deer, the temporal glands of the elephant, the facial glands of the bat, the pedal glands of ruminants, the lateral glands of the shrew-mouse, the sacral glands of the peccary, the caudal glands of the desman, the preputial glands of the musk-deer and beaver, etc. These glands are often found near the anus or in the inguinal region and then often open into special cutaneous pits, e.g. the anal glands of many Carnivora, Rodentia, and Edentata, the civet gland of the Viverridae, the musk pouch of *Moschus* and the preputial glands of the male beaver. The lacrymal glands may also be placed in the category of cutaneous glands.

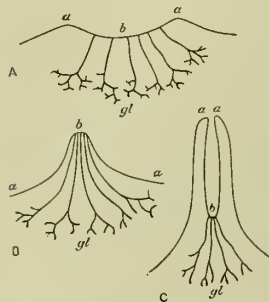


FIG. 258.—Diagrams showing the different kinds of nipple/mammary gland with in mammals (from Gegenbaur). A the monotreme condition. B the true teat. C the false teat: *a* periphery of glandular area; *b* glandular area (mammary pouch); *gl* glands.

The mammary glands occur in all mammals. In monotremes they are said to be modified sweat glands, but in all other mammals there can be little doubt that they are modified sebaceous glands. In monotremes they open on a slight depression of the skin called the mammary areas or pouches (Fig. 258). In many mammals this area is much deepened and the surrounding skin rises up around it to form the *teat*, in this case called a false teat, of

the gland (Ruminantia, Carnivora, etc., Fig. 258). In others there is no mammary pouch, but the area of skin on which the glands open is simply raised into a papilla, the so-called true teat (primates, marsupials, Fig. 258). The position and number of the mammary glands vary considerably.

The skeleton consists of heavy bones, usually containing marrow.

The skull (Figs. 259, 260) differs from that of reptiles in the following features. The primordial cartilage is completely ossified and the separate bones, which are fewer than in reptiles, meet and are separated only by sutures, which in old animals tend to disappear. In a few cases the bones become fused in early life (*Monotremata*). There are no prefrontal or post-frontal bones, and no membrane bone in the floor corresponding

to the parasphenoid. There is only one temporal arcade formed of the jugal and zygomatic process of the squamosal and corresponding either to the lower temporal arcade of reptiles or to the upper and lower temporal arcades combined into one and not perforated by a lateral temporal fossa.

The maxillary and palatine bones are firmly united with the skull, and there is a hard palate formed by palatal plates of the premaxilla, maxilla and palatine, and occasionally, as in crocodiles, by the pterygoid (some cetaceans and edentates). The pterygoid, so conspicuous in the lower forms, is a small scale-like bone connected with the palatine but without relation with the suspensorial region.

The quadrate has been absorbed into the squamosal so that the lower jaw articulates with the squamosal direct. The articular surface for the condyle of the lower jaw is called the glenoid cavity. The squamosal enters largely into the side wall of the skull. The lower jaw consists of the fused articulare and dentary and is formed of one piece on each side. The petrotic consists of the petrous portion (petrosal) in the skull (Fig. 260, *Pe*) and the mastoid portion which appears on the surface between the exoccipital and the squamosal (Fig. 259, *Pe*) ; it ossifies from three centres which constitute the epiotic, prootic and opisthotic elements ; these unite with each other before joining any neighbouring bones. The petrotic usually unites with the squamosa and the tympanic to form the temporal bone. The tympanic bone (*Ty*) is a membrane bone which frequently forms the floor and front wall of the tympanic cavity and may be prolonged outwards in a tubular or spout-like manner, bounding the bony external auditory meatus. It is often considerably swollen to form the *tympanic bulla*. The complex of bones, called the temporal, fills in a gap in the skull wall between the exoccipital and the alisphenoid, leaving only a small unfilled portion in front and behind. The former is called the *foramen lacerum medium basis cranii* and transmits the internal carotid artery ; the latter is larger and constitutes the *foramen lacerum posterius basis cranii* which transmits the internal jugular veins, and the 9th, 10th, and 11th cranial nerves.

The occipital bone always articulates with the atlas vertebra by two condyles, and its lateral portions frequently possess a

well-marked process on each side, the paroccipital or jugular (paramastoid) processes (*Pm*). The base of the skull is well ossified in cartilage bone. The basisphenoid (*Spb*) usually remains distinct from the presphenoid (*Ps*) for a considerable time. Its upper surface is hollowed out as the pituitary fossa (*sella turcica*) which lodges the pituitary body. The alisphenoid (*Als*) and parietals (*Pa*) complete the basisphenoid section of the skull and the orbitosphenoid and frontals (*Ors*, *Fr*) the presphenoid region. There is no interorbital septum, and the ethmoid with its perforated or cribriform plate (*lamina cribrosa*) constitutes the anterior boundary of the cranial cavity. In the Primates only

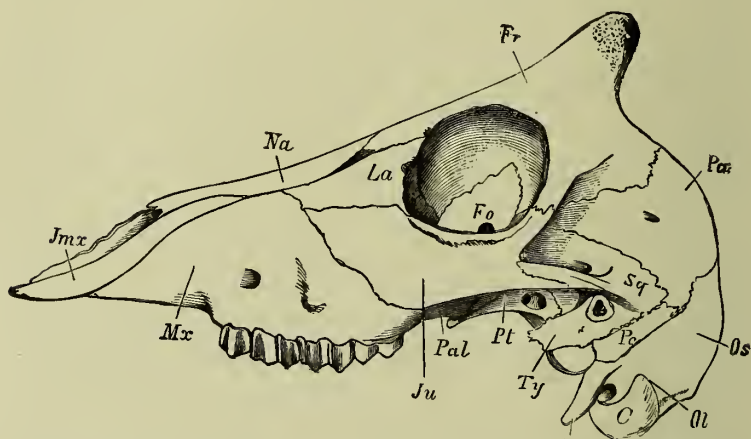


FIG. 259.—Skull of a goat, from the side (from Claus). *C* occipital condyle, *Fo* optic foramen, *Fr* frontal, *Jmx* premaxilla, *Ju* jugal, *La* lacrymal, *Mx* maxilla, *Na* nasal, *Ol* exoccipital, *Os* supraoccipital, *Pa* parietal, *Pal* palatine, *Pe* mastoid portion of petrosal, *Pm* paroccipital process, *Pt* pterygoid, *Sq* squamosal, *Ty* tympanic.

do the lateral parts of the ethmoid (*lamina papyracea*) take part in forming the inner wall of the orbit. In all other cases the ethmoid is placed in front of the orbit and its lateral portion (*os planum*) is covered by the maxillae. Two parts may be distinguished in the ethmoid, (1) a median plate (*lamina perpendicularis*) which is continued in front into the cartilaginous nasal septum and is underlaid by the vomer and covered dorsally by the nasals, (2) the lateral masses. The lateral masses of the ethmoid, or spongy bones as they are called, result from the ossification of the complexly folded cartilage of the nasal capsule, over the surface of which the terminal fibres of the

olfactory nerves are spread. On their outer sides these laminae are connected by a thin plate of bone, the *os planum*, which usually lies as above stated against the inner wall of the maxillae. Behind they are all connected together to form the sieve-like cribriform plate which is joined to the hind end of the median ethmoid and blocks up the anterior end of the cranial cavity. The *os planum* and the ossified laminae constitute together the *lateral mass* of the ethmoid bone above referred to. The laminae are usually divided into two sets, which, though all parts of the same bone, have received different names according to their mode of attachment to neighbouring bones. These are the ethmoturbinal (superior and middle turbinals, Fig. 260, *C*) and

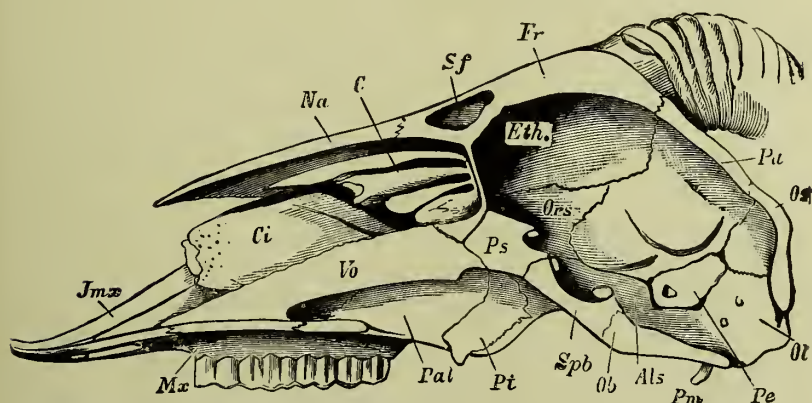


FIG. 260.—Median longitudinal section of a sheep's skull (from Claus). *Als* alisphenoid; *C* ethmoturbinal, *Ci* maxilloturbinal, *Eth.* ethmoid, *Fr* frontal, *Jmx* premaxilla, *Mx* maxilla, *Na* nasal, *Ob* basioccipital, *Ol* exoccipital, *Ors* orbitosphenoid, *Os* supraoccipital, *Pa* parietal, *Pal* palatine, *Pe* petrosal, *Ps* presphenoid, *Pt* pterygoid, *Sf* frontal sinus, *Spb* basisphenoid, *Vo* vomer. The median plate of the ethmoid is not seen.

the maxillo-turbinal (*Ci*). The uppermost lamellae of the ethmoturbinals lie immediately beneath the nasals and are frequently united to them; they constitute the so-called *naso-turbinal*. The maxillo-turbinals (inferior turbinals) are the portions lying farther forward: they owe their name to the fact that they unite with the maxillae. The maxillo-turbinal being placed farther forwards lies in the direct current of respiratory air and its mucous membrane is not innervated by the olfactory nerve, but by the fifth nerve. The lateral masses of the ethmoid are generally held to correspond with the pre-

frontals of the lower types. The lacrymal bone (absent in the *Pinnipedia* and some *Cetacea*) is placed in the anterior wall of the orbit, and often also appears as a facial bone on the face (Fig. 259, *La*).

The most important foramina in the cranial wall are, typically, as follows. (1) The perforations in the cribriform plate which transmit the fibres of the olfactory nerve. (2) The optic foramen in the orbitosphenoid. (3) The foramen lacerum anterius (sphenoidal fissure), a space between the orbitosphenoid and alisphenoid, which transmits the 3rd, 4th, 6th cranial nerves and the anterior division of the 5th. (4) The foramen rotundum and (5) the foramen ovale, both perforations of the alisphenoid which transmit respectively the second and third divisions of the 5th nerve. (6) The foramen lacerum medium between the alisphenoid and the petiotic (just internal to the opening of the bony eustachian passage) for the passage of the internal carotid artery. (7) On the inner surface of the petiotic is the opening of the meatus auditorius internus which transmits the auditory and facial nerves, the former to terminate in the walls of the membranous labyrinth, the latter to traverse the bone and emerge by (8) the stylomastoid foramen, which is placed immediately behind the bulla and just anterior to the paroccipital process. (9) The foramen lacerum posterius between the petiotic and exoccipital for the 9th 10th and 11th nerves and the internal jugular vein. (10) A foramen in the exoccipital just in front of the condyle, called the *condylar foramen*, for the transmission of the 12th nerve. (11) The foramen magnum by which the spinal cord enters the skull.

The alisphenoid canal, present in some mammals, is a horizontal canal in the alisphenoid at the root of the pterygoid process, through which the external carotid passes in part of its course; it begins behind just in front of the foramen ovale and ends in front at the foramen rotundum.

The brain so completely fills the cranial capsule in the Mammalia that the internal surface of the skull presents a relatively accurate impression of its surface. Owing to the considerable size of the brain the cranial capsule is far more spacious than in any other class of Vertebrata; but it presents great variations in this respect in the different groups, being smallest in some of the extinct orders.



The prominence of the facial part of the skull also varies greatly. It may be said, speaking generally, to vary inversely with the development of the intellectual faculties. The condition of the skull in this respect is expressed by reference to the *cranio-facial angle*, which is the angle between the basicranial axis, i.e. the line drawn from a point midway between the occipital condyles through the median plane of the skull to the junction between the ethmoid and presphenoid, and the facial axis, i.e. the line drawn from the anterior end of the premaxilla to the anterior end of the basicranial axis. When the face projects straight out in front of the cranium this angle is nearly  $180^\circ$ , i.e. the two axes are nearly in the same straight line; when on the other hand the face lies below the anterior end of the cranium it is less and in man approaches a right angle. The first condition, viz. that of projecting face and large facial angle, is known as *prognathism*, the other condition, in which the facial angle is smaller, is called *orthognathism*.

The hyoid bone is reduced to a transverse bar (body) carrying two pairs of cornua.

The vertebral column, except in the Cetacea, is divided into five regions, viz. cervical, thoracic, lumbar, sacral and caudal (Fig. 261). In the aquatic Cetacea, which are without hind limbs, the lumbar region passes gradually into the caudal; on the other hand the cervical region is strikingly shortened, and the fusion of its anterior vertebrae renders it rigid and immovable. The vertebral bodies are only exceptionally (neck of Ungulates) connected by articular surfaces, but are usually joined by elastic discs (intervertebral ligaments). The first cervical vertebra (atlas) is a bony ring with broad, wing-like, transverse processes. The axis has an odontoid process. The dorsal vertebrae are characterised by high, crest-like, spinous processes, and by the possession of ribs. The anterior ribs are attached by cartilage to the sternum, which is usually elongated and composed of a number of bony pieces arranged one behind another; the posterior ribs (the so-called "false ribs") do not reach the sternum. The ribs articulate with the vertebrae by means of a capitulum and tuberculum. The first piece of the sternum, which is sometimes keeled (bats, moles, etc.), is called the manubrium; the last piece is called, as in the lower types, the xiphoid process or ensiform cartilage. In monotremes alone

is there a distinct interclavicle (episternum). While the number of cervical vertebrae is almost constantly seven, that of the dorsal vertebrae is subject to a greater variation. As a rule there are thirteen, sometimes twelve dorsal vertebrae; but there is a less number in some bats and armadillos, while there are fifteen or more in some animals. The horse has eighteen, the rhinoceros and elephant nineteen to twenty, and the three-toed sloths have twenty-three to twenty-four. The lumbar vertebrae, which have long lateral processes in place of ribs, are usually seven in number. The number rarely sinks to two as in *Ornithorhynchus* and the two-toed sloths, and still more rarely rises to eight or nine (*Stenops*). The sacral vertebrae,

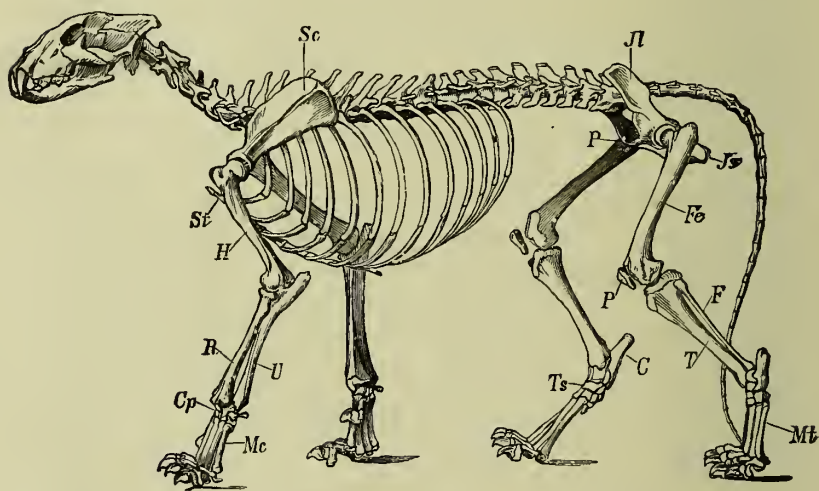


FIG. 261.—Skeleton of the Lion (after Giebel). *C* calcaneum; *Cp* carpus; *F* fibula; *Fe* femur; *H* humerus; *Il* ilium; *Is* ischium; *Mc* metacarpus; *Mt* metatarsus; *P* patella; *P* pubis; *R* radius; *Sc* scapula; *St* sternum; *T* tibia; *Ts* tarsus; *U* ulna.

which vary in number from two (marsupials) to four, more rarely nine (*Armadillo*), are firmly united with one another, and by their transverse processes (with the rudiments of the ribs) with the iliac bones. In whales and Sirenia there is no union of vertebrae to form a sacrum. The caudal vertebrae, which vary considerably in number and mobility, become narrower towards the end of the axis of the body, and often (kangaroo and ant-eaters) possess inferior spinous processes (chevron bones or

intercentra) ; but all the processes become less and less conspicuous towards the posterior extremity.

The outer surface of the scapula is traversed by a ridge called the spine which divides it into a prescapular and postscapular portion. The spine usually projects at the lower end as the acromion process, from which a backwardly directed process, the metacromion, may arise. The anterior pair of extremities is never absent. The clavicle is absent when the anterior limbs serve only for the support of the anterior part of the body in locomotion, or perform simple, pendulum-like movements, as in swimming, walking, running, jumping, etc. (Cetacea, Ungulata, Carnivora). Otherwise the acromion process of the scapula is connected with the sternum by a more or less strong, rod-shaped clavicle. The coracoid is almost always reduced to the coracoid process of the scapula ; in the Monotremata only is it a large bone which reaches the sternum. The posterior extremities are more firmly connected with the body than are the anterior. In the Cetacea and Sirenia alone is the pelvic girdle rudimentary, and is represented by two rib-like bones which are quite loosely connected with the vertebral column. In all other mammals the pelvic girdle is fused with the lateral parts of the sacrum, and is closed ventrally by the symphysis of the pubis and sometimes also of the ischium (except in a few Insectivora). The three bones are always united into one, the *os innominatum*, which is pierced in the ischio-pubic region by a fontanelle called the obturator foramen (corresponding to the coracoid fenestra of the shoulder girdle of some lower types). The appendages articulated to the pectoral and pelvic girdles are considerably shortened in the swimming Mammalia, and either constitute, as in the Cetacea, flat fins, the bones of which are immoveable upon one another (in the Sirenia there is a joint at the elbow), and in which there is a great number of phalanges, or, as in the Pinnipedia, have the form of fin-like legs, which can also be used in locomotion on land. In the Chiroptera (bats), the anterior limbs present a large surface in consequence of an expansion of the integument (patagium) uniting the limbs with the sides of the body, and extended between the elongated fingers.

In the land Mammalia the extremities present considerable variations both in their length and special structure. The

humerus often has a foramen above the inner condyle called the entepicondylar foramen. Its presence is supposed to be a primitive feature, as it is chiefly found in the lower and older (extinct) forms. It is characteristic of some ancient reptiles e.g. Hatteria, Anomodontia, etc. The radius and ulna in the fore-limb and the tibia and fibula in the hind-limb are almost always longer than the humerus and femur respectively. The ulna forms the hinge-joint of the elbow, and is prolonged at this point into a process called the olecranon; the radius, on the other hand, is connected with the carpus, and can often be rotated round the ulna (pronation, supination); in other cases it is fused with the ulna, which then constitutes a rudimentary, styliform rod continued from the olecranon process. In the hind-limb the knee-joint projects forwards, and is usually covered by a knee-cap, the patella; the fibula is sometimes (marsupials) moveable on the tibia, but as a rule these two bones are fused, and the fibula which is placed posteriorly and externally is usually reduced.

The variations in the terminal parts of the limbs are far more striking (Fig. 262). The number of digits is never greater than five, and is often less. The order of their disappearance has already been described (p. 480).

In the carpus of Mammalia the three proximal bones remain distinct, a centrale is occasionally present (*Hyrax*, many Insectivora, Primates, etc.) and carpalia 4 and 5 of the distal row are always fused together. There is always a radial sesamoid developed in the tendon of the flexor muscles and called the *pisi-form*. There may also be a smaller ulnar sesamoid. The names given to these bones are shown in the following table, with the equivalent terms used by Comparative Anatomists.

Radiale	=	Scaphoid	(Naviculare).
Intermedium	=	Lunar	(Semilunare).
Ulnare	=	Cuneiform	(Triquetrum).
Centrale	=	Centrale	(Intermedium).
Carpale 1	=	Trapezium	(Multangulum majus).
Carpale 2	=	Trapezoid	(Multangulum minus).
Carpale 3	=	Magnum	(Capitatum).
Carpale 4	}	Unciform	(Hamatum).
Carpale 5			

In stating the number of the carpal bones the pisiform is generally included, so that a carpus with a centrale is said to consist of nine bones, without a centrale of eight.

The radial and ulnar sesamoids have been regarded as vestiges of extra digits, viz. of a prepollex and postminimus respectively. Another view is that the radial sesamoid is in reality the radiale, the scaphoid being a second centrale. It cannot be said that these views are generally held, but it may be noted that occasionally the radial sesamoid is double and bears a nail-line structure (*Pedetes caffer*).

It frequently happens that when the digits are reduced in number, the persisting metacarpals and metatarsals, to which the single name **metapodium** may for convenience' sake be given, are elongated, or even fused together to form the so-called **cannon bone**.

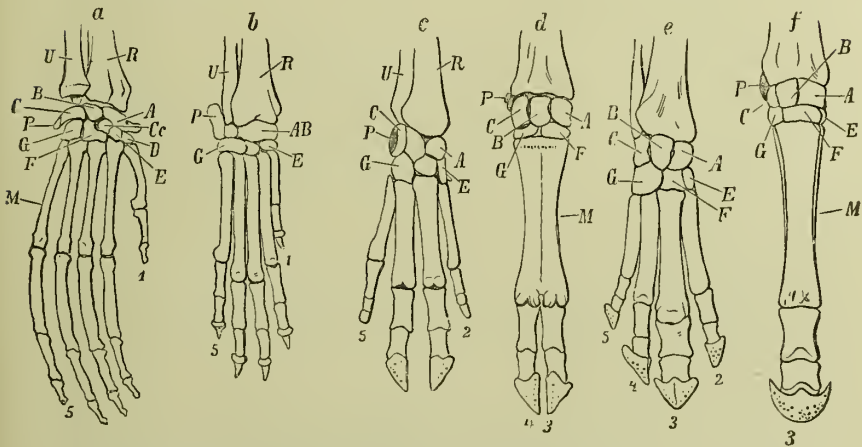


FIG. 262.—Skeleton of the manus of *a* orang, *b* dog, *c* pig, *d* ox, *e* tapir, *f* horse (from Claus). A scaphoid; B lunar; C cuneiform; D trapezium; E trapezoid; F magnum; G unciform; P pisiform; U centrale; M metacarpus; 1-5 digits numbered.

The number of phalanges characteristic of the Mammalia has already been given (p. 480).

The *ungual* phalanges are the terminal phalanges which bear the claws, nails, or hoofs. A *plantigrade* animal is one which places the whole of the lower surface of the manus (carpus, metacarpus, phalanges) or pes on the ground in walking. The term *digitigrade* is applied when the two distal phalanges only are applied to the ground, the first phalanx and the metapodia being vertical. When the last phalanx and hoof alone carry the weight the animal is said to be *unguligrade*. There are also



conditions intermediate between these, to which such terms as *semiplantigrade*, *semidigitigrade* have been applied.

In the tarsus the tibiale and intermedium are always fused (according to the ordinary view), the centrale is always present, and tarsalia 4 and 5 are fused as are the corresponding bones in the wrist. Tibial and fibular sesamoids are very generally present, but the tibial sesamoid is not so important as the pisiform of the wrist. But, as in the case of the manus, sesamoid bones may be developed in tendons in other situations, as in the tendons on the plantar surface of the tarsus, on the plantar surface of the metatarso-phalangeal articulation.

The following table shows the names of the tarsal bones.

Tibiale	}	= astragalus (talus).
Intermedium		
Fibulare		= calcaneum (os calcis).
Centrale		= navicular (scaphoideum).
Tarsale 1		= internal cuneiform (entocuneiform).
Tarsale 2		= middle cuneiform (mesocuneiform)
Tarsale 3		= external cuneiform (ectocuneiform).
Tarsale 4	}	= cuboid.
Tarsale 5		

The ankle joint is always between the crus (tibia and fibula) and the tarsus, never between the two rows of tarsal bones as in birds and some reptiles; and the calcaneum always possesses a well-marked heel process.

The **nervous system** is characterised by the size and high development of the cerebrum, the hemispheres of which are so large that they not only fill the anterior part of the cranial cavity but even partly cover the cerebellum (Fig. 263). In *Ornithorhynchus*, various small rodents and insectivores and some of the smaller primates the surface of the hemispheres is smooth or nearly so (Fig. 263, *a*), but in most Mammalia it is marked by depressions and ridges, which in the higher forms (Fig. 263, *d*) become furrows or fissures (*sulci*) and convolutions (*gyri*). The number and complexity of the convolutions may be said, speaking generally, to vary directly with the intelligence of the animal, but they seem, in some cases at least, to depend upon the size of the animal, for we frequently find that in the smaller members of a group the convolutions are less marked than in the larger.

They reach their highest development in the *Cetacea*, the brain of which is even more complexly convoluted than that of man. A broad commissure, the *corpus callosum*, connecting the two hemispheres is always present except in Monotremata and Marsupialia. When this is absent the anterior commissure is large, and there is an important commissure taking the place of the body of the fornix and called the hippocampal commissure. The latter is placed just above the anterior commissure. The lateral ventricles possess anterior and descending cornua, and in the *Cetacea* and *Primates* a posterior cornu as well.

The optic lobes, which are four in number and known as the *corpora quadrigemina*, are reduced in size and are in great part or entirely covered by the posterior lobes of the hemispheres (Fig. 263). The pituitary body (*hypophysis*) and the pineal body (*epiphysis*) are always present. There is no parietal organ. The cerebellum consists of a median lobe or vermis and of two lateral lobes each of which carries a small accessory lobe, the *flocculus*. A transverse commissure, the *pons varolii*, lying on the ventral surface of the anterior part of the medulla oblongata and connecting the lateral lobes of the cerebellum, is always present, but varies in its development in the different forms. There are twelve pairs of cranial nerves as in *Sauropsida*. The spinal cord usually extends only as far as the sacral region where it ends with a *cauda equina*; there is no posterior rhomboidal sinus.

**Sense organs.** The sense of touch is most acute in the skin of the face, lips, tongue and ends of the extremities, the skin in these regions being provided with special organs in which the nerves terminate called *tactile corpuscles*. The *vibrissae* or long bristle-like tactile hairs which are often found on the face, and the papillae of which are richly innervated, are special organs of touch. In the same category may be placed the wings and the cutaneous expansions on the faces of bats, which are so sensitive as to enable the animal to detect obstacles without touching them, by the mere alteration in the pressure of the air in their neighbourhood.

The sense of **taste** has its seat principally at the root of the tongue (*papillae circumvallatae*) and on the soft palate.

The sense of **smell** appears to be present in all Mammals

except the toothed whales in which there are no olfactory nerves. It is effected by the mucous membrane which covers the ethmo-turbinal bone of the nasal labyrinth; it is in this mucous membrane that the olfactory nerve fibres terminate. The two nasal

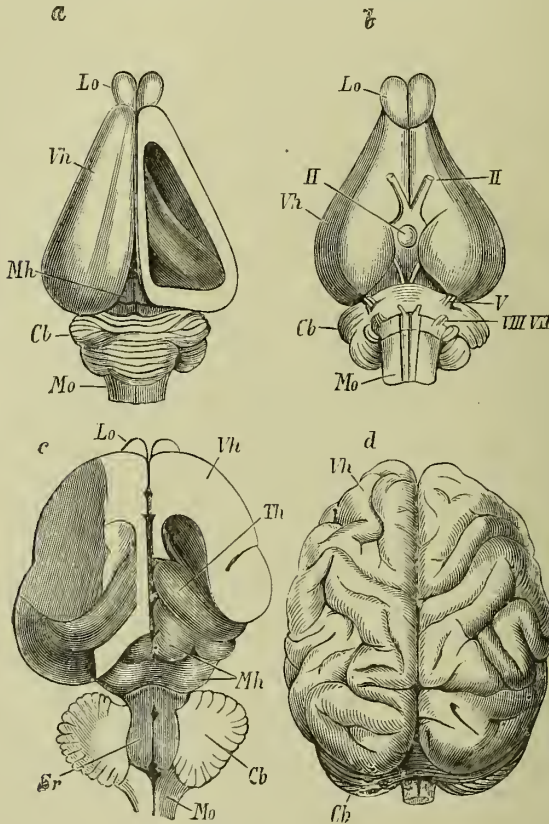


FIG. 263.—Mammalian brains (from Claus). *a* brain of rabbit, dorsal view; the roof of the right hemisphere is cut away, so as to expose the lateral ventricle. *b* the same from below. *c* brain of cat; on the right side the lateral and posterior part of the hemisphere has been removed, and almost as much on the left side, and the greater part of the cerebellum has been removed. *d* brain of orang. *Cb* cerebellum; *H* hypophysis cerebri; *Lo* olfactory lobe; *Mh* corpora quadrigemina; *Mo* medulla oblongata; *Sr* sinus rhomboidalis; *Th* optic thalamus; *Vh* cerebral hemispheres; *V* root of trigeminal nerve; *II* roots of optic, *VII*, *VIII* of facial and auditory nerves.

cavities, which are separated by the median nasal septum, communicate with the nasal passages passing from the external nostrils to the internal narial openings. They also often communicate with spaces in the adjacent cranial and facial bones

(*sinus frontales, sphenoidales, maxillares*). In the *Cetacea* the external nostrils are sometimes united to form a single opening. The nasal openings are often placed at the end of a prolongation of the face, which is sometimes greatly developed, as in the trunk of the elephant. In the aquatic mammals they can be closed by muscles or a valvular apparatus. *Jacobson's organ* is present in many mammals (Marsupialia, Edentata, Insectivora, Carnivora, Ungulata), in the form of two tubes placed ventrally to the septum nasi and receiving a branch of the olfactory nerve. They generally join Stenson's duct and so open into the mouth.

The **eyes** present the normal vertebrate structure. Their most noticeable features are perhaps the presence of retinal bloodvessels and the absence of any structure corresponding to the pecten. They are always much reduced and may be quite vestigial in burrowing animals. In some rodents and insectivores (*Talpa, Chrysochloris*) and in the marsupial *Notoryctes* they are hidden beneath the skin, and in the freshwater cetacean *Platanista* they are very imperfectly developed. Both upper and lower lids, which are usually covered with hair, are present, and in addition there is a third transparent eyelid at the inner angle of the eye, the nictitating membrane. The nictitating membrane is absent in Primates where it is represented by the *plica semilunaris*, and in the *Cetacea*. The cornea is fairly convex in most forms, but flattened in the *Cetacea*. There is a tapetum, which reflects the light, in the choroid coat in many mammals (Carnivora, Ungulata, etc.).

Both harderian and lacrymal glands are present in most Mammalia (absent or reduced in the whales, and reduced in the Pinnipedia). The lacrymal gland has several openings on the conjunctival surface beneath the upper lid towards the posterior (outer) side of the eye; the harderian gland (which lies at the inner side of the eyeball and mainly on its lower surface, opens in connection with the nictitating membrane at the inner angle. The harderian gland is absent in Primates. The nasal ducts open on the *puncta lacrymalia* of which there are two at the inner angle of the eye one above and one below the *caruncula lacrymalis*. These two ducts join to form the nasal duct which opens into the nasal passage. The meibomian glands are sebaceous glands placed in the lids beneath the conjunctiva and opening on the free edges of the latter.

The auditory organ differs from that of the Sauropsida principally in the greater development of the external auditory meatus and of the external ear (*pinna*), in the greater number of sound-conducting bones (*malleus*, *incus*, *stapes*), in the presence of the organ of Corti, and except in Monotremata in the spiral winding of the cochlea and the absence of a papilla acustica lagenae. The ductus endolymphaticus proceeds from the narrow canal connecting the saccule and the utricle; it perforates the periotic bone, enters the cranial cavity and ends in the dura mater in a small dilatation, the saccus endolymphaticus. The auditory nerve has six terminations, the papilla acustica lagenae and the macula neglecta being absent. The windings of the cochlea vary in number from  $1\frac{1}{2}$  in *Erinaceus europaeus* to 5 in *Coelogenys paca*.

The tympanic cavity is more spacious than in the lower forms, being frequently swollen into the *bulla ossea* which is formed by the alisphenoid in the Marsupialia, and by the os tympanicum in other forms. It communicates with the pharynx by a wide opening in Monotremata, but in other Mammalia there is a long eustachian tube. It is also in communication with cavities in the adjacent bones (air-cells of the mastoid, etc.).

The stapes is usually perforated, but it is columelliform and unperforated in Monotremata, *Perameles*, *Manis* and some other Mammalia. The homologies of the mammalian auditory ossicles have been much disputed.\* By Huxley the stapes was regarded as the columella auris of the Sauropsida and the incus as the suprastapedial part of the same structure (see especially *Sphenodon*). On this view the malleus is the homologue of the quadrate. Others regard the malleus as the os articulare, the incus as the quadrate and the stapes as the columella. Finally it is held by some anatomists that the whole chain of ossicles is comparable to the columella auris and its various processes of the Sauropsida, the quadrate appearing in mammals as the os tympanicum.

Huxley's view is based largely upon the arrangement of the parts in *Sphenodon*, and upon the fact that in the mammalian embryo, the processus gracilis of the malleus is continuous with Meckel's cartilage.

\* Huxley, On the representatives of the malleus and incus of the Mammalia in the other Vertebrata. *P. Z. S.*, 1869. Gadow, "On the modifications of the first and second visceral arches," *Phil. Trans.*, 179.



Huxley considered the suprapetrotal (mammalian incus) to be homologous with the hyomandibular or top of the hyoid arch of fishes (hence its connection with the malleus which he regards as the proximal end of the mandibular arch in mammals), the stapes or columella affording a secondary connection with the petrotic capsule. By the upholders of the view that the malleus, incus, and stapes are all differentiations of the columella auris of reptiles (top of the hyoid arch) the connection of the processus gracilis of the malleus with Meckel's cartilage in the mammalian embryo would be regarded as secondary, and as another example of the arrangement in the Crocodilia in which Meckel's cartilage is connected with the columella by a cartilaginous band (p. 376). We are inclined to accept the last view so far as the homologies of the ossicles are concerned, but we differ in thinking that the quadrate has been absorbed into the squamosal in mammalia (pp. 399, 479) and has nothing to do with the tympanic, which is largely a membrane bone.

**Dentition.** Teeth are entirely absent in the adults of some mammals, e.g. whalebone whales, the monotremes, many edentates, but in many of these small calcified teeth, which do not cut the gums but are absorbed early, are found in the foetus. *Echidna* and some of the American ant-eaters appear to be as edentulous as birds, no trace of teeth having been found even in the foetus. When present they may be found on the premaxillae, maxillae and mandibles, never on the palatal bones. They are imbedded in sockets in the bone, (thecodont) the *dental alveoli*, which are lined by a vascular membrane, the alveolar dental membrane. They do not become ankylosed to the jaws. The part of the tooth which projects above the gum is called the *crown*; the part below the gum and embedded in the socket is called the *root* or *fang*. The neck of the tooth is where the root and crown join. The back-teeth (grinders) commonly have more than one root embedded in separate sockets, and this occasionally applies to some of the anterior teeth (some Insectivora, etc.). The tooth contains a central pulp-cavity which has an opening at the apex of the root, or, if there are more roots than one, at the apex of each root (Fig. 264, III, IV). This cavity contains a connective tissue pulp with bloodvessels and nerves. In young growing teeth and in the so-called rootless teeth which grow throughout life (Fig. 264, I), the openings of the pulp cavity are wide, but they become narrow when growth has ceased and the pulp becomes relatively less important; pulp, however, usually persists throughout life conferring sensibility on the dentine which is traversed by the protoplasmic processes of the cells which line

the pulp cavity (odontoblasts). These processes are continued in the dentinal tubes of the dentine and only extend into the enamel in rare cases.

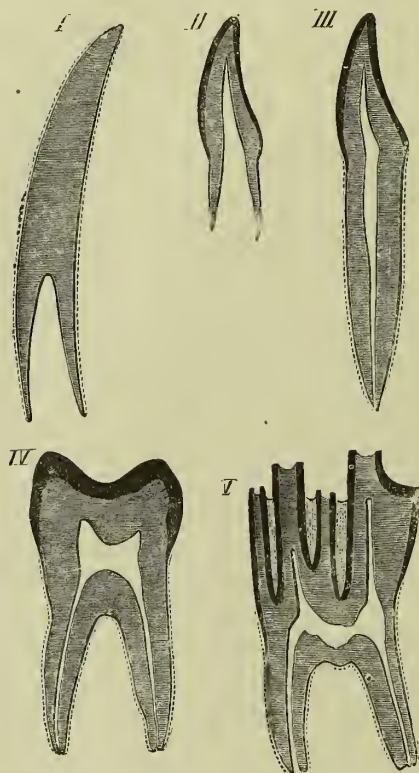


FIG. 264.—Diagrammatic sections of various forms of teeth. *I* Incisor (tusk) of elephant with pulp cavity persistently open at the base. *II* Human incisor during development with tooth imperfectly formed and pulp cavity widely open at base. *III* Completely formed human incisor with pulp cavity contracted to a small aperture at the apex of the root. *IV* Human molar with broad crown and two roots. *V* Molar of the ox with long tubercles or as it is sometimes described, with the enamel covering the crown deeply folded and the depressions filled in with cement; the surface is worn by use; in the unworn tooth the enamel would be continuous at the tops of the ridges. In all the figures, the enamel is black, the pulp white, the dentine represented by horizontal lines, and the cement by dots (after Flower and Lydekker).

The teeth consist of dentine, which is covered by enamel on the crown and by a thin layer of cement, which has the structure of bone, on the root (Fig. 264). Occasionally cement is found outside the enamel on the crowns (see below). In a few cases, e.g. most edentates, the tusks of elephants, enamel is entirely or almost entirely absent. The dentition of mammals is almost always *heterodont*, i.e. it consists of different kinds of teeth in different parts of the jaws. There are commonly four kinds of teeth in each jaw. There are : the *incisors* in front ; they are usually chisel-shaped and in the upper jaw are the only teeth placed in the premaxillae : next to the incisors and often separated from them by a gap, called *diastema*, come the *canines* ; these are never more than one on each side in each jaw ; they are al-

most always strong conical projecting teeth and are developed in (or behind) the premaxillo-maxillary suture : the canines are followed by the *grinding teeth* or back-teeth, which are almost

always in a continuous series, but frequently separated by a diastema from the canines. The anterior grinding teeth are called the *premolars*, the posterior are the *molars*. The grinding teeth have usually more complex crowns than the anterior teeth, and the premolars have nearly always simpler crowns than the molars. The distinction between them is least marked in herbivorous animals, in which the posterior premolars at least resemble the molars. Speaking generally it may be said that there is a serial increase in complexity in proceeding from the front to the hind end of the premolar-molar series. But this does not always apply: in some forms, e.g. many Carnivora, the hinder molars are smaller and less complex than the teeth immediately in front of them. The molars are usually distinguished from the premolars not only by their more complicated crowns, but also by the fact that they have no functional predecessors in the milk dentition (but are only formed once in the life of the animal). This brings us to another characteristic feature of the mammalian dentition. Most mammals are *diphyodont*, i.e. they have two functional sets of teeth and never more than two sets. Occasionally there is only one set

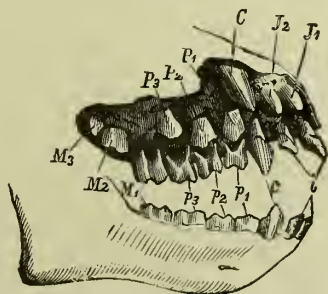


FIG. 265.—Dentition of *Cebus* while changing the teeth (from Claus, after Owen). The small letters point to the milk teeth, the capital letters to the permanent teeth.

(toothed whales, many edentates, etc.) which last through life: in this case they are said to be *monophyodont*. When there are two sets, the first set is called the *milk* or *deciduous dentition*, because it is usually found in the young animal during the period of active growth. Typically the milk teeth are shed as the jaws attain their full size and are replaced by the permanent dentition (Fig. 265). The first back tooth of the permanent dentition to appear is usually the first molar, which in consequence presents a more worn appearance than the later appearing posterior molars. This frequently gives us a means of determining the limit between the premolars and the molars, when the posterior premolars resemble the molars in the form of their crowns, as they sometimes do.

A dental formula is a short way of expressing the number and

kinds of teeth present. In the normal complete mammalian dentition, which is found in but few living mammals (e.g. *Sus*, *Gymnura*, *Talpa*, *Myogale*) there are on each side and in each jaw three incisors, one canine, four premolars, and three molars. This is expressed by the formula :  $i \frac{3}{3} \quad c \frac{1}{1} \quad p \frac{4}{4} \quad m \frac{3}{3} = 44$ . In such a case the deciduous dentition would consist of three incisors, one canine, and four molars on each side in each jaw and the formula would be written thus :  $di \frac{3}{3} \quad dc \frac{1}{1} \quad dm \frac{4}{4} = 32$ . Frequently however the first premolar in the complete mammalian dentition has no predecessor in the milk series (a few ungulates and *Hyra*x may be mentioned as cases in which there are four milk molars), so that the milk dentition would be,  $di \frac{3}{3} \quad dc \frac{1}{1} \quad dm \frac{3}{3} = 28$ . Sometimes the dental formula is written more fully, so that each tooth receives its special number, thus :— $i \frac{1.2.3.}{1.2.3.} \quad c \frac{1}{1} \quad p \frac{1.2.3.4.}{1.2.3.4.} \quad m \frac{1.2.3.}{1.2.3.}$ . This method of writing the formula enables us to express our views shortly as to the homologies between teeth in different animals, in which the full number of teeth are not formed. Thus the first premolar of the permanent dentition, the tooth which frequently has no predecessor in the milk dentition (it is disputed however whether this tooth belongs to the milk or to the permanent series) often falls out very early. We could express its absence thus :  $p \frac{0.2.3.4.}{0.2.3.4.}$ .

Such determinations must not however be pressed too far, as it is usually quite impossible to determine homologies between teeth of the same category in different dentitions, as has been shown by Bateson,\* and sometimes it is even difficult to determine whether a tooth as distinctive as the canine is present or absent. The canine tooth in the upper jaw is the first tooth in the maxillary bone, and the canine in the lower jaw is the tooth which bites in front of this. But as the first premolar may simulate a canine in appearance and the real canine may simulate an incisor, it is sometimes difficult to be certain as to whether we are dealing with a canine or not. The canine may be looked upon as the first tooth of the premolar series ; it is usually but not always enlarged and caniniform in appearance.

If it is difficult in doubtful cases to settle whether a tooth so distinctive as a canine is present, much more difficult must it be to decide which tooth of a given category is absent, in cases in which the full number is not present. It is usual to assume that the incisors are diminished from the posterior end, i.e. if there are only two, it is the 3rd incisor which has gone.

\* *Materials for the Study of Variation*, London, 1894.



In the same way the molars are supposed to be cut off at the hind end of the series also, but if the premolars are incomplete it is the anterior which are supposed to be missing. No doubt these are rules in some cases, but there are many cases in which they do not apply, as will be seen in the account of the different orders.

The anterior milk molars as a rule resemble premolars in the permanent dentition, while the hind milk molars are molar-like in form.

The dentitions of the Cetacea, Edentata, and Marsupialia present important variations from the normal mammalian arrangements. For a description of them we refer the reader to the systematic account of these orders.

Much might be written about the form of teeth. We must content ourselves with the following remarks. The incisors are generally chisel-shaped, with a cutting edge; the canines conical and pointed; the premolars compressed and either conical or cutting; the molars with broad crowns and crushing. But the posterior premolars frequently resemble or approximate to the molars in form. There is frequently a ridge round the base of the crown just above the neck called the *cingulum*. The crown of the premolars is frequently elongated antero-posteriorly and provided with smaller accessory cusps, as a rule one on each side of the main cusp or tubercle. Such a three-cusped tooth with the cusps all in one plane is called *triconodont*. Sometimes the three cusps are not arranged in a line, but in a triangle, the teeth of the upper jaw having one inner and two outer cusps; those of the lower jaw having two inner and one outer cusp. This form is called the *tritubercular* (sometimes *trigonodont*): it is more commonly found amongst the molars than the premolars. It is frequently complicated by the addition of a posterior heel or *talon* (Fig. 283) which may have one or two cusps. Such a form of tooth which is usually in the molar series is called *tubercular-sectorial*. Further additional cusps may be developed between the three primary cusps. Most commonly there is one such additional cusp, so that if the tooth has no talon it becomes quadricuspidate, the cusps or tubercles being arranged in an anterior and in a posterior pair. To these four cusps one or two may be added; if one, it may be placed between the cusps of the posterior pair, or between those of the anterior pair; if two, one of them is between the cusps of the anterior and the other between the cusps of the posterior pair.



We thus get the 5-cusped and 6-cusped teeth, which are usually in the molar series. Finally the teeth may have more than six cusps, in which case they are *multicuspidate*. When there is a well marked talon the anterior part of the tooth has typically, though not always, three cusps arranged in the triangular manner.

Professors Cope and Osborn \* have endeavoured to show that all cusped mammalian grinding teeth may be referred to the tritubercular tooth, usually with the addition of a cusp-carrying talon (*tubercular-sectorial*). The cusps in this supposed primitive tooth and on its talon have been named, and their homologies with the cusps of different mammalian teeth determined. In this manner a theory of very great complexity, called the *tritubercular theory* or simply *trituberculism* has been elaborated. Without offering any opinion as to the validity of this theory, we have decided not to make use of it in this work, because the facts of tooth structure in the different orders can be made sufficiently clear without it, and because it does not appear to us to render that assistance in reducing the facts to order which would justify us, at present, to ask the student to make the considerable effort needed to master its complexities.

Such grinding teeth in which the crown is elevated into blunt or pointed cusps are called *bunodont* teeth. It frequently happens however that the cusps are spread out in one direction at the base and connected by ridges. These ridges commonly run transversely across the tooth, and when they are well developed the crown of the tooth appears to be traversed by ridges of enamel; such teeth are called *lophodont*. In some cases the cusps or tubercles are flattened at the base and spread out in a crescentic manner (as in *Ruminantia*). The crowns of such teeth appear to be traversed by crescentic ridges of enamel arranged of course partly in a longitudinal and partly in a transverse direction. Such teeth are called *selenodont*. Lophodont and selenodont teeth are found in herbivorous animals in which the food, often dry and hard, requires much mastication. They are thus subjected to considerable wear and the projecting enamel on the crown becomes worn down. In this way the tops of the cusps and ridges become worn off and the dentine exposed, and the crowns of the teeth appear to be traversed by laminae of enamel containing between them exposed dentine. It is clear that when the crown is short, a tooth exposed to such hard wear must soon be worn down to the neck. To obviate this, it frequently happens that the crown, with its tubercles and cusps,

\* Trituberculy, *Amer. Nat.*, 1897, p. 993.

is much elongated vertically, the neck of the tooth being deeply imbedded in the socket. Such long crowned teeth are called *hypsoodont* in contradistinction to the first described teeth with short crowns which are called *brachyodont*. It is evident that to render a hypsoodont tooth effective, it must gradually rise in its socket as the crown is worn down. This is sometimes partly effected by continued growth at the base of the tooth, the pulp cavity remaining open and the pulp active. But hypsoodont grinding teeth are rarely rootless throughout life. They are often rootless in the young animal, continuing to grow for a time, but as a rule the roots are soon formed and growth ceases. In such cases the subsequent elevation of the tooth to meet the continual wear of the crown is effected in a manner which is not fully understood.

Hypsoodont teeth are found constantly in some groups of the *Ungulata*. In the *Rodentia* in which they also often occur, considerable variety is found, closely allied species differing in this respect.

In hypsoodont teeth the cusps and ridges are of course much elongated vertically, and there are deep chasms and valleys between them. These are usually filled with cement (Fig. 264, V), which confers strength and holds the elongated tubercles together. The result of this is that the surface of the worn tooth presents a pattern caused by the three materials of different degrees of hardness which compose the crown. These patterns consist of the laminae of hardest material, enamel, bounding areas of the next hardest substance, the dentine, and surrounded by the softer cement which pervades the whole crown between the cusp and ridges.

**Development of teeth** (Fig. 266). There is formed in the embryo at a comparatively early stage of development an ingrowth, in the form of a double lamina, of the lower layer (stratum Malpighi) of the buccal epithelium. This ingrowth extends along the whole length of the jaws and constitutes the *primitive tooth-band*. There is frequently a groove in the lining of the mouth placed immediately over it and called the dental groove (zf); this, however, appears to be without significance in the tooth development.

The tooth-band has at first the appearance of a tubular gland projecting into the subjacent mesoblast. The definitive tooth-

germs are formed as buds from the outer (labial) side and near the free end of this structure (Fig. 266, *A*). The first formed of these buds give rise to the milk teeth. As soon as the rudiments of these are established the free edge (*zl*) of the tooth-band grows deeper into the subepithelial mucosa and gives rise, on its labial side as before, to a second series of buds: these are the rudiments of the permanent teeth (Fig. 266, *B*, *C*). Inasmuch as the deeper part of the tooth-band becomes inclined inwards towards the middle line the first formed buds and the tooth-germs developed from them lie on the labial (outer) side of the buds formed later. Each of the epithelial buds formed from the outer lamina of the tooth-band gives rise to the *enamel organ* (*se*, *sp*, *sm*) of a tooth and ultimately loses its connection with

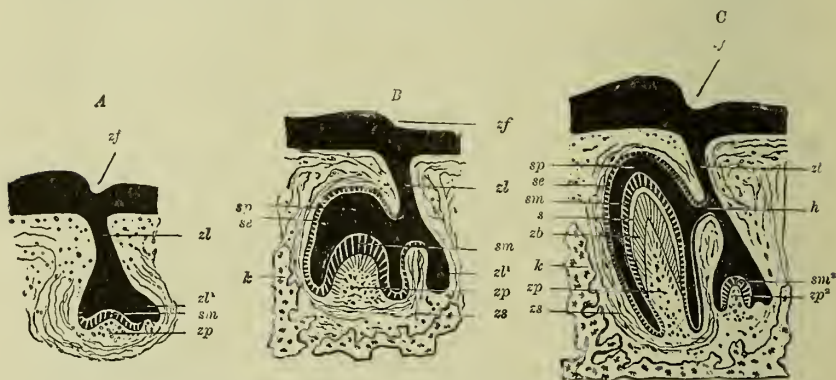


FIG. 266.—*A*, *B*, *C*, Three stages in the development of a milk and permanent tooth of a mammal in diagrammatic section (after O. Hertwig). *h* neck by which the enamel organ of the milk tooth is connected with the tooth-band; *k* bone of dental alveolus; *s* enamel; *se*, *sm* inner and outer epithelium of enamel organ; *sm*<sup>2</sup> inner epithelium of enamel organ of permanent tooth; *sp* enamel pulp; *zf* dental furrow; *zl* tooth-band; *zl'* free deep end of tooth-band, from which the permanent tooth will be developed; *zp* dental papilla; *zs* dental sac; *zp*<sup>2</sup> dental papilla of the permanent tooth; *zb* dentine.

the tooth-band. The conversion of a bud into an enamel organ is associated with the formation of a *dentine-papilla* or *dentine-germ* (*zp*) which gives rise to the dentine of the tooth and the cement of the root. The process is as follows: the bud becomes swollen at its end, and then bell-shaped, the concavity of the bell being directed *inwards*, i.e. away from the lining of the mouth. The subepithelial mesoblastic tissue in the concavity of the bell is the dentine-papilla. We thus get a bell-shaped enamel organ (Fig. 266, *C*) consisting of ingrown buccal epithelium, connected by a narrow stalk (*h*) with the tooth-band and

placed upon a papilla-shaped dentine germ which is derived entirely from the mesoblast. The subsequent formation of the enamel from the enamel organ, of the dentine and cement from the dentine-germ, and of the tooth-sac from the adjacent mesoblastic tissue are fully described in works dealing with histology and development to which we must refer the reader.

In addition to the tooth-germs of the milk and permanent dentitions, already described, other tooth-rudiments, which never attain full development, are formed in many mammals.\* These are developed as buds from the outer side of the tooth-band in precisely the same way as are the rudiments of the functional teeth. There is usually only one set of these vestigial rudiments, the relation of which to the rudiments of the functional teeth varies in different mammals. In marsupials, the pig, and the guinea-pig, the vestiges in question are formed from the tooth-band *before* the rudiments of the milk-teeth and lie on the labial side of these. In the seals, hedgehog, dog, and man they arise *after* the rudiments of the permanent teeth and lie on their lingual side. In the former case these buds are regarded as vestiges of a *prelacteal* dentition, in the latter of a *postpermanent* series of teeth. In those groups, such as the Cetacea and Marsupialia in which the dentition is functionally monophyodont or nearly so, and in which traces of two or three dentitions can be made out there is some dispute as to which of these dentitions the functional teeth belong to, as is shown in the subjoined table. In man there are said to be four sets of tooth-rudiments, viz. of the prelacteal vestigial dentition, of the milk and permanent dentitions, and of the postpermanent vestigial series. In short it would appear that in Mammalia there are traces of four dentitions, of which never more than two become functional.† To this extent the dental condition of mammals may be said to approximate to the polyphyodont condition of reptiles.

If the four dentitions of Mammalia be called premilk, milk,

\* Leche, *Entwick. d. Zahnsystems der Säugethiere*, *Bibliotheca Zoologica*, 1895. Küenthal, *Jena. Zeitschrift*, 28, 1894, p. 76. Röse, *Das Zahnsystem der Wirbelthiere*, *Ergebnisse, d. Anatomie u. Entwickl.*, 1894. Wilson and Hill, *Q.J.M.S.*, 39, 1897, p. 427. Adloff, *Jena. Zeitschr.*, 32, 1898, p. 347. Marett Tims, *Journal Anat. and Physiol.*, 36, 1902, and 37, 1903. M. F. Woodward, *P. Z. S.*, 1893, p. 450, and 1896, p. 557.

† It has recently been stated that in the extinct Toxodont, *Nesodon*, there were possibly three functional incisor dentitions (W. B. Scott, British Association, Cambridge meeting, 1904).

permanent, and post-permanent, respectively, the present state of our knowledge with regard to their occurrence may be expressed by the subjoined table, in which *v* indicates vestigial and *f* functional dentitions.

	Number of Den- titions.	Premilk.	Milk.	Perma- nent.	Post Perma- nent.	View of.
Marsupialia	3	v	f	v	absent	Leche, Deppendorf, M. Woodward etc.
" . . .	"	absent	v	f	v	Wilson, Hill, Tims, etc.
Cetacea (toothed)	2	absent	f	v	absent	Kükenthal.
" . . .	"	absent	v	f	absent	Tims.
Seal . . .	3	absent	f	f	v	Leche, Kükenthal.
Hedgehog and Dog	"	absent	f	f	v	M. Woodward, Tims.
Pig . . .	3	v	f	f	absent	Adloff.
Guinea-pig .	3	v	f	f	absent	Adloff.
Man . . .	4	v	f	f	v	Röse, Tims.

The vestiges on the labial side of the permanent molars clearly belong to the milk series (which in Diphyodonts erupt in the anterior part of the mouth). The presence of these vestiges raises the question as to whether there is any morphological distinction between the premolar and molar series. For the homology of the replaced tooth of marsupials the reader is referred to the systematic account.

In most lower Vertebrata the succession of teeth appears to be indefinite, and except in Teleostei all the teeth are formed, as in mammals, from a tooth-band, the inner end of which continues to grow and produce new buds on the lingual side of those last formed. In the Teleostei the successive teeth appear to be in many cases formed independently from the buccal epithelium and not from a tooth-band.

**Alimentary Canal.** In addition to the hard structures at the entrance to the digestive cavity, soft moveable lips which bound the mouth opening, and a fleshy tongue which is of very various form and lies on the floor of the buccal cavity, are of special importance for the prehension and preparation of the food (Fig. 267). In the Monotremata the lips are replaced by the edges of the beak. The tongue, however, is never absent, but it may be immoveable, and completely fused with the floor of the mouth, as in the whales. Its front part is mainly tactile in function, but in some cases it is used to seize (giraffe) or capture food (ant-eaters). Various shaped papillae, which are often cornified and bear recurved hooks, project from its upper



surface. The papillae circumvallatae alone have a relation to the sense of taste. The tongue is supported by the hyoid bone and by a cartilaginous rod, which represents the os interglossum. The anterior cornua of the hyoid are attached by ligament to

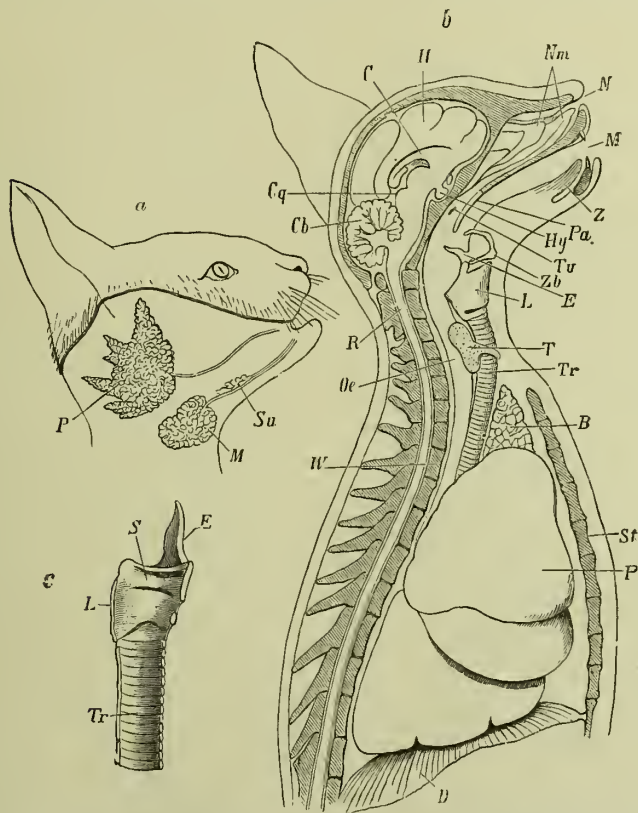


FIG. 267.—Entrance to the digestive apparatus and the respiratory organs of the cat (after C. Heider). *a* head with exposed salivary glands. *P* parotid; *M* sub-maxillary; *Su* sub-lingual. *b* Longitudinal section through the head and thorax; the respiratory organs are seen from the side. *c* Longitudinal section through the larynx (*L*) and the first part of the trachea (*Tr*). *B* thymus; *C* corpus callosum; *Cb* cerebellum; *Cq* corpora quadrigemina; *D* Diaphragm; *E* epiglottis; *H* cerebral hemispheres; *Hy* hypophysis; *L* larynx; *M* mouth; *N* nasal aperture; *Nm* turbinal bones; *Oe* oesophagus; *P* lung; *Pa* velum palati; *R* spinal cord; *S* vocal cord; *St* sternum; *T* thyroid; *Tr* trachea; *Tu* opening of eustachian tube into the pharynx; *W* vertebral column; *Z* tongue; *Zb* hyoid.

the styloid processes of the temporal bone or its equivalent, the posterior bear the larynx. Beneath the tongue there is sometimes (most developed in the Insectivora) a single or double projection, which is termed the *sublingua*. The sides of the buccal cavity are soft and fleshy, and are not unfrequently in

the rodents, apes, etc., dilated into wide sacs—the so-called cheek-pouches. The soft palate (*palatum molle*) must be mentioned as a structure peculiar to the Mammalia; it constitutes the boundary between the buccal cavity and pharynx. All mammals, with the exception of the carnivorous Cetacea, have salivary glands,—a parotid, a submaxillary, and a sublingual,—the fluid secretion of which is poured out in large quantities, especially in herbivorous forms. The oesophagus, which follows the wide gullet, only exceptionally presents crop-like dilations; it is usually of considerable length, and opens into the stomach behind the diaphragm. The stomach is, as a rule, a simple transversely placed sac, but is frequently divided by the gradual differentiation and constriction of its anterior, lateral, and posterior regions into a number of parts, which are most completely separated in the ruminants and distinguished as four separate stomachs. The pyloric region is principally distinguished by the presence of gastric glands, and is more or less sharply separated from the beginning of the small intestine by a sphincter muscle and by an inwardly projecting fold (pyloric valve). The intestine is divided into a small and a large intestine, the boundary between which is indicated by the presence of a valve and a caecum, which is especially developed in herbivorous animals. The anterior part of the small intestine, or duodenum, contains the so-called Brunner's glands in its mucous membrane, and receives the secretion of the large liver and the pancreas. The liver is multilobed, and is sometimes without a gall bladder. When a gall bladder is present the bile duct (*d. cysticus*), and the hepatic duct (*d. hepaticus*) unite to form a common duct (*d. choledochus*). The small intestine is longest in animals which eat grasses and leaves, and is characterised by the numerous folds (*valvulae conniventes*) and villi of its mucous membrane, and by the possession of a great number of groups of glands (Lieberkuhn's) and by Peyer's patches which are composed of adenoid tissue. The terminal region of the large intestine or rectum opens, except in the Monotremata which are characterised by the possession of a cloaca, behind the urinogenital opening, though the two openings are sometimes surrounded by a common sphincter (Marsupialia, some Insectivora and Pinnipedia).

The heart (Fig. 268) of Mammalia, like that of Birds, is divided into a right venous and a left arterial portion, each with a ven-

tricle and auricle (sometimes as in *Halicore* the division is marked externally). It is enclosed in a pericardium, and sends off an arterial trunk, which forms a left aortic arch, from which two vessels frequently arise, viz. (1) a right anonyma, with the two carotids and right subclavian; and (2) the left subclavian; or, as in man, three vascular trunks, viz. (1) a right anonyma, with the right carotid and right subclavian; (2) the left carotid; and (3) the left subclavian, all close to one another. As a rule, one superior vena cava (right) and an inferior vena cava open into the right auricle; more rarely, as in the rodents, monotremes, and elephants, etc., there are two superior venae cavae. Retia mirabilia have been recognised principally for the arterial vessels, and are found on the extremities of burrowing and climbing animals (*Stenops*, *Myrmecophaga*, *Bradypus*, etc.); on the carotids round the hypophysis, and on the ophthalmic arteries in the orbit in ruminants; finally on the intercostal arteries and the iliac veins of the dolphin. The red blood

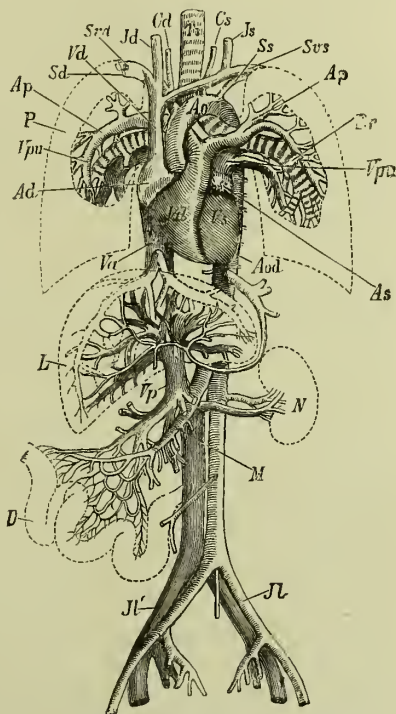


FIG. 268.—Circulatory apparatus of man (from Owen, after Allen Thomson). Aa right auricle; Ao aortic arch; Aod descending aorta; Ap pulmonary artery; As left auricle; Br bronchi; Cd right carotid; Cs left carotid; D intestine; Jd right jugular; Js left jugular; L liver; M mesenteric artery; N kidney; P lungs; Sd right subclavian artery; Ss left subclavian artery; Srd right subclavian vein; Svs left subclavian vein; Tr trachea; Va inferior vena cava; Vd superior vena cava; Vpu pulmonary vein; Vs left ventricle.

corpuscles are devoid of a nucleus and are discoidal, except in the Camelidae in which they are elliptical. They vary in size: in man they are  $\frac{1}{3200}$ th of an inch; in the elephant  $\frac{1}{2700}$ th of an inch; they are smallest in the chevrotains in which they are

about  $\frac{1}{12000}$ th of an inch. A renal-portal system is always absent, and in no Mammalia, except *Echidna*, is there an anterior abdominal vein carrying blood to the liver.

The lymphatic system is provided with numerous lymphatic glands, and its main trunk (ductus thoracicus), which is placed on the left, opens into the left brachiocephalic vein.

Of the so-called vascular glands the **spleen**, the **thymus**, and the **thyroid**, which is especially developed in the young, are very generally present.

The **body-cavity** of mammals is distinguished by the fact that the two anterior horns, which in *Amphibia* and many *Reptilia* extend forwards on each side of the pericardium, are cut off from the general body cavity and constitute the closed pleural cavities. The diaphragm or midriff, a muscular partition with a central tendinous portion, is developed in the tissue placed between the pleural and pericardial cavities and the abdominal cavity. Abdominal pores are never present and the kidney tubes never have nephrostomata.

The paired lungs (Fig. 268, *p*) are freely suspended in the thoracic cavity, and are distinguished by the numerous ramifications of the bronchial tubes, the finest branches of which end with conical, funnel-shaped dilations (infundibula), which are provided on their lateral surfaces with swellings. Respiration is mainly effected by the movements of the diaphragm, which forms a complete, usually transversely placed, septum between the thoracic and abdominal cavities: by the contraction of its muscular parts it acts as an inspiratory muscle; that is, it dilates the thoracic cavity. The elevation and depression of the ribs also have an effect in dilating the thorax. The trachea is, as a rule, straight, without coils, and divides at its lower end into two bronchi leading to the lungs. There may be, in addition, a small accessory (third) bronchus on the right side. The trachea is supported by cartilaginous half-rings which are open dorsally, and only exceptionally by complete rings of cartilage. The first part of the trachea, or larynx, is placed at the lower end of the pharynx, behind the root of the tongue; it is supported by the posterior horns of the hyoid bone, possesses vocal chords, complicated pieces of cartilage (cricoid, thyroid, and arytenoid cartilages) and muscles, and constitutes a vocal organ.

In the Cetacea alone is the larynx, which projects in the base

of the pharynx as far as the posterior nares, used exclusively for respiration. A moveable epiglottis (almost tubular in the Cetacea), attached to the upper edge of the thyroid cartilage, projects over the glottis. When food is being swallowed it sinks and closes the glottis. Accessory cavities, with membranous or cartilaginous walls, are sometimes attached to the larynx. These sometimes function as air reservoirs, e.g. the air-sacs of *Balaena*, sometimes as a resonating apparatus for the strengthening of the voice, as in many monkeys (*Myctes*). In many mammals the nasal passages are connected with air-spaces in the bones of the head (frontal, ethmoidal, maxillary bones, etc.), and the tympanic cavity communicates with air-sinuses in the mastoid.

The kidneys (Fig. 268, *N*) sometimes consist (seals, dolphins) of numerous lobes united together at the pelvis of the kidney. As a rule, however, they are compact bean-shaped glands, lying in the lumbar region, outside the peritoneum. The ureters arise from the so-called pelvis of the kidney, and always open, except in Monotremata, into a urinary bladder, placed in front of (ventral to) the intestine. The duct of the bladder joins the ducts of the generative organs, and forms a urogenital canal called vestibule in the female and unethra in the male, opening ventral to the anus. Anterior to the kidneys there is a glandular organ termed the suprarenal body.

The male sexual organs (Fig. 269) of most Mammalia are characterized by the change in the position of the testes. In only a few cases (Monotremata, Cetacea, etc.) do the testes remain near the kidneys; in most mammals they descend in front of the pelvis, and, pushing the peritoneum before them, enter the inguinal canal (many rodents), or, still more frequently, pass through the inguinal canal into a cutaneous fold, which is transformed into the scrotum. Not unfrequently (rodents, bats, insectivores) they pass back through the open inguinal canal into the abdominal cavity after the breeding season: this is affected by the cremaster, a slip of muscle separated from the oblique abdominal muscle. The scrotum, as a rule, lies behind the penis; but in the marsupials it is formed by an invagination of the integument directly at the entrance of the inguinal canal in front of the male copulatory organ. The coiled excretory ducts of the testes, which are derived from the wolffian body and ducts,



constitute the epididymis, and lead into the two vasa deferentia, which, after forming glandular dilations (seminal vesicles), open close together into the urethra. At this point open the ducts of the prostates, which differ much in form, and are often divided into several groups of glands. Further down a second pair of

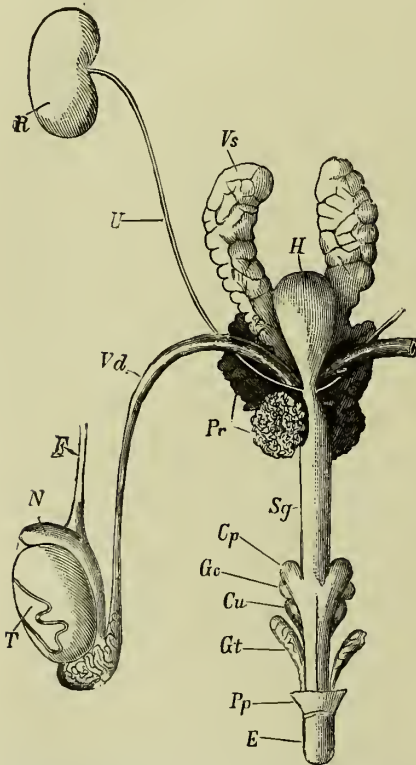


FIG. 269.—Urinary and sexual organs of *Cricetus vulgaris* (after Gegenbaur). *Cp* corpora cavernosa penis; *Cu* corpus cavernosum urethrae; *E* glans penis; *F* funiculus spermaticus (spermatic cord); *Gc* Cowper's glands; *Gt* Tyson's glands; *H* urinary bladder; *N* epididymis; *Pp* prepuce; *Pr* prostate; *R* kidney; *Sg* urogenital sinus (urethra); *T* testis; *U* ureter; *Vd* vas deferens; *Vs* vesiculae seminales.

glands, known as Cowper's glands, opens into the urethra. Remains of the müllerian ducts, which in the female are used as the oviducts, frequently persist between the openings of the vasa deferentia. They are called the organ of Weber (uterus masculinus), and in the so-called hermaphrodites their parts are much enlarged, and may be differentiated in the manner peculiar to the female sex. In all cases the end of the urethra, which functions as a urinogenital canal, is in connection with external copulatory organs: these always have the form of an erectile penis, which, in the Monotremata, is concealed in a pouch in the cloaca. The penis is supported by cavernous erectile bodies, which in the Monotremata are confined to paired corpora

cavernosa urethrae; but in all other Mammalia there are, in addition to the corpus cavernosum urethrae (*c. spongiosum*) which is unpaired and surrounds the urethra, two upper corpora cavernosa penis, which are attached to the ischium, and only rarely fuse with one another. A cartilaginous or bony support,

the so-called os penis (Carnivora, Rodentia), may also be developed, especially frequently in the glans. The glans, which is formed by the corpus cavernosum urethrae (Fig. 269, *E*), and which is bifid only in exceptional cases (Monotremata, Marsupialia,) varies greatly in its form, and lies retracted in a reduplication of the skin (foreskin or prepuce) which is richly glandular (gl. tysonianae).

**Female sexual organs.** The ovaries (Fig. 270) are unsymmetrical only in the Monotremata, in consequence of the reduction of the right ovary. In all other cases they are equally

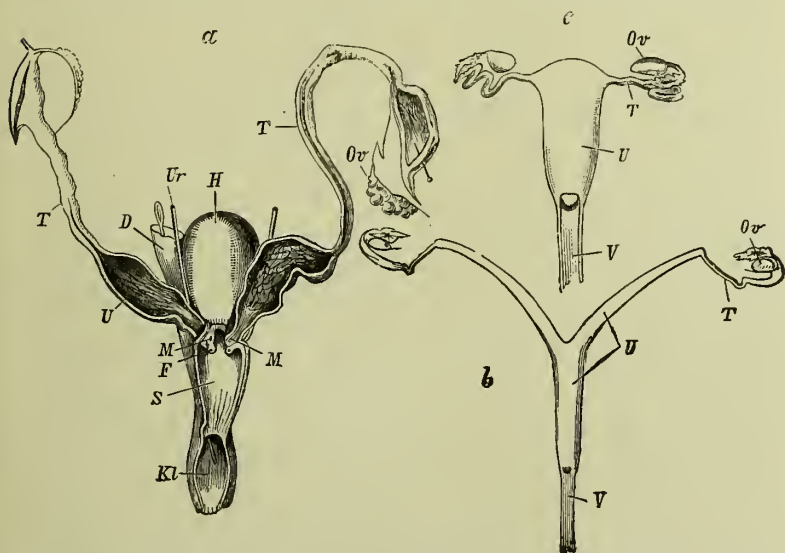


FIG. 270.—Female generative organs. *a* of *Ornithorhynchus* (after Owen); *b* of *Viverra genetta*; *c* of *Cercopithecus nemestrinus*; *D* intestine; *F* opening of ureter; *H* urinary bladder; *Kl* cloaca; *M* mouth of uterus; *Ov* ovary; *S* urinogenital sinus; *T* oviduct; *U* uterus; *Ur* ureter; *V* vagina. A style is passed through the opening of the intestine into the cloaca in *a*.

developed on either side; they are placed in folds of the peritoneum, close to the funnel-shaped dilated mouths of the oviducts, by which they are sometimes completely surrounded. The oviduct is divided into (1) the fallopian tube, which is always paired and begins with a free ostium; (2) the dilated, sometimes paired, more frequently unpaired, middle portion—the uterus; and (3) the terminal part, or vagina, which is unpaired, except in marsupials, and opens behind the opening of the urethra into the short urinogenital sinus, or vestibule. In the Monotremata the

two tubular uteruses open, without forming a vagina, on papilliform prominences into the urinogenital sinus, which is still connected with the cloaca (Fig. 270).

According to the different degrees of duplicity of the uterus (when a vagina is present), we may distinguish: the uterus duplex, with more or less complete external separation and double os uteri (rodents, marsupials); the uterus bipartitus, with single os uteri, but almost complete internal partition (rodents); the uterus bicornis (Fig. 270, *b*), in which the upper parts, or horns of the uterus are separate (Ungulata, Carnivora, Cetacea, Insectivora); and finally the uterus simplex (Fig. 270, *c*) with single cavity and very muscular walls (Primates).

The vestibule, with its glands of Duvernoy (Bartholin), which correspond to the Cowperian glands of the male, is separated from the vagina by a constriction, and in *Homo* also by a fold of the mucous membrane, called the hymen. The external generative organs consist of the labia majora and labia minora, at the sides of the sexual opening, and of the clitoris. The labia majora are two external folds of skin, and are equivalent to the two halves of the scrotum; the labia minora are two smaller internal folds, and are not always present. The clitoris possesses erectile tissue and a glans, and is the equivalent of the penis. The clitoris may sometimes (as in *Ateles*) reach to a considerable size and be perforated by the urethra (rodents, moles, lemurs). In such cases of perforated clitoris, there is, of course, no common urinogenital sinus. Morphologically, the female genitalia represent an earlier stage of development of the male organs, which, in the cases of the so-called hermaphrodite formation, may in consequence of arrest of development preserve a more or less female structure. As a rule the two sexes are easily distinguished by the different form of the external generative organs. Frequently there is a marked dimorphism in the whole external appearance; the male being larger, having a different hairy covering, being possessed of a louder voice, and provided with stronger teeth or special weapons (horns). On the other hand, the milk glands, which are situated in the inguinal region, on the abdomen, and on the thorax, and which almost always project into teats or nipples, are rudimentary in the male sex.

There is, in Mammalia a breeding period which may be called

the sexual season.\* In males this season is characterized by testicular activity and sexual excitement, and is generally called *rut*. In females the matter is more complicated. In them the sexual season comprises a series of phenomena which constitute the "*oestrus cycle*." The typical course of the oestrus cycle is as follows. It begins (1) with a congestion of the external generative organs which spreads to the uterus and leads to (2) a growth which causes a thickening of the mucosa. This is followed by (3) a rupture of the capillaries and extravasation of blood into the uterine mucous membrane, which extravasated blood in some cases (Primates, some Rodentia, Ungulata and Carnivora, etc.), in consequence of tissue degeneration, finds its way into the uterus and thence to the exterior. This phenomenon is in the Primates known as the menstrual flow.† The uterus then rapidly heals and the last stage (4) of the cycle is reached. This is known as the oestrus or period of desire. During it copulation takes place and the cycle comes to an end.

The different stages of this cycle, the first three of which constitute the *prooestrus*, vary in their severity in different animals, and in some of them, as stated above, the extravasated blood does not break through the mucosa and the menstrual flow of blood does not occur, but the homology of the phenomena throughout the series is undoubted.

**Ovulation** is supposed to take place at some period during the oestrus cycle, but the course of this phenomenon is not fully understood and there is probably considerable variation in it, in different animals and even in the same animal, at different periods of life. In some cases (e.g. ferrets, domestic rabbits) the stimulus of copulation seems necessary to bring about ovulation; e.g. in the domestic rabbit ovulation occurs  $9\frac{1}{2}$  hours after copulation. In other cases, probably the majority, ovulation is independent of copulation and takes place in its absence during some period of the oestrus cycle (in bitches it takes place during the external bleeding or later). The case of the bat is peculiar. In this animal the sexual season occurs in the

\* W. Heape, "The sexual season of Mammals and the relation of the prooestrus to menstruation, *Q.J.M.S.*, vol. 44, 1901, p. 1. F. H. A. Marshall, "The oestrus cycle and the formation of the corpus luteum in the sheep, *Phil. Trans.*, 1903, p. 47.

† W. Heape, "The menstruation of *Semnopithecus entellus*, *Phil. Trans.*, 1894. Id., "The menstruation and ovulation of *Macacus rhesus*," *Phil. Trans.*, 1897.

autumn and copulation then takes place, but it is not until spring that ovulation occurs, so that the spermatozoa live all the winter in the uterus. It is recorded, however, that young female bats experience their sexual season in the spring (compare the case of *Salamandra*, p. 307).

The occurrence and frequency of the sexual season also vary to a considerable extent in different mammals. In many it occurs more than once in each year, in others not more than once in two years. Climatic and nutritive conditions are important factors in determining its onset and periodicity, and there is considerable variation in accordance with local conditions even amongst individuals of the same species. Thus woodland deer breed earlier than those which live above the tree-level, and foxes at a high altitude breed later than those which live in the plains. Walruses, which are compelled to expend their energies for twelve months in feeding their calf, breed only once in two years. Scarcity of food and a rigorous climate tend to reduce sexual activity, while the luxury attending domestication results in greatly increased breeding powers.

The graafian follicle after expelling its ovum becomes filled with cells and is called the *corpus luteum*. This structure undergoes a series of changes which differ (*Homo*) according to the occurrence or non-occurrence of gestation. Considerable importance has been ascribed to these changes (ovarian secretion \*), and it is said that destruction of the corpus luteum by electric cautery or other means will bring about cessation of development and degeneration of the uterine foetus.

The ova of the Mammalia were first discovered by C. E. von Baer. They are extraordinarily small (with very little yolk) and are surrounded by a strongly refractile membrane (*zona radiata*), round which a layer of albumen is sometimes deposited in the oviduct.

The fertilization appears to take place in the oviduct (fallopian tube), and segmentation, which except in Monotremata is complete, is effected either in the oviduct (rabbit, mole, etc.) or in the uterus (ferret, sheep, etc.). Amnion and allantois are present. In the uterus the embryo becomes connected with the uterine wall by means of its outer epithelial layer, now known as the **trophoblast**. This, later, becomes coated wholly or in part on its inner side by somatic mesoblast and constitutes the membrane known as the subzonal membrane (false amnion and

\* Marshall, *op. cit.*



somatic wall of yolk-sac of avine embryos, Fig. 271, *Sh*). Later on, the mesoblast of the peripheral part of the allantois becomes applied to the subzonal membrane and the two structures

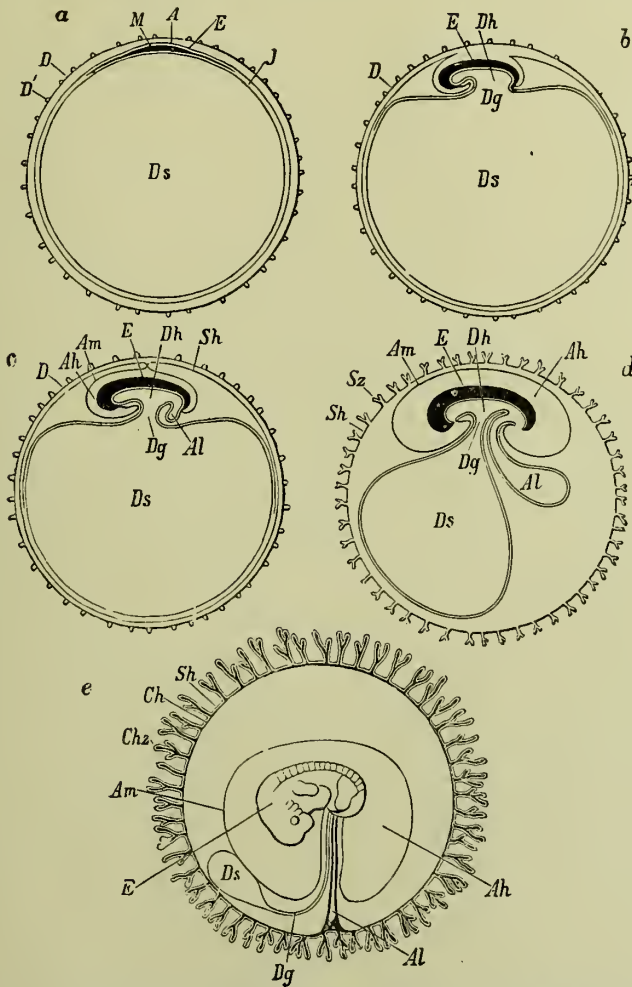


FIG. 271. Diagrammatic figures illustrating the formation of the foetal membranes of a mammal (after Kölliker). *a* embryo before appearance of amnion; *b* embryo with yolk-sac and developing amnion; *c* embryo with amnion closing and developing allantois; *d* embryo with villous subzonal membrane, and with mouth and anus; *e* embryo in which the vascular layer of the allantois is applied to the subzonal membrane, and has grown into the villi of the latter, yolk-sac reduced, the amniotic cavity is increasing; *A* embryonic thickening of the external layer; *Ah* amniotic cavity; *Al* allantoic stalk; *Am* amnioti; *Ch* chorion; *Chz* chorionic villi; *D*, *D'* zona radiata; *Dg* umbilical stalk; *Dh* intestinal cavity; *Ds* cavity of the embryonic (blastodermic) vesicle, later of the yolk-sac (umbilical vesicle); *E* embryo; *J* embryonic thickening of the inner layer, *M* of the middle layer; *Sh* subzonal membrane (serous envelope); *Sz* villi of subzonal membrane.

constitute the embryonic membrane called the *chorion* (Fig. 271 *e, ch*). The chorion develops vascular villi which enter into close relation with the uterine wall. In this manner there is developed a relatively large surface, permeated with branches from the foetal vessels, the blood of which is in intimate osmotic connection with the blood of the uterine wall. This connection of the chorion of the foetus with the uterine walls gives rise to the *placenta*, by means of which the nourishment and respiration of the foetus are provided for in the body of the mother. The placenta is wanting only in the Monotremata and most Marsupialia, which, therefore, have been called Aplacentalia, as opposed to the rest of the Mammalia, which have a placenta and have been called Placentalia. The placenta presents great variations in the individual orders, in its special development and in the mode of its connection with the uterine walls. Either the villi of the placenta are loosely connected with the uterine walls, and separate from the latter at birth (Adeciduata), or they become so intimately united with the uterine mucous membrane that the latter comes \* away with the embryo at birth, as the decidua or after-birth (Deciduata). In the first case the villi may be numerous and uniformly distributed over the whole chorion (diffuse placenta of Ungulata, Cetacea, etc.), or be aggregated in special places, forming small tufts, the so-called cotyledons (ruminants). In the other case, the placenta with its villi is confined either to an annular zone on the chorion (pl. annularis or zonary placenta of Carnivora, Pinnipedia), or to a discoidal area (metadiscoidal placenta of man and apes, discoidal placenta of rodents, insectivores, bats).

The trophoblast of the mammalian embryo is a structure of great physiological importance. It is the layer in relation with the uterine wall, and in the early stages is employed in secreting fluid into the cavity of the blastodermic vesicle and so facilitating the nourishment of the embryo in the earliest stages. Later, it is the layer by which the attachment of the embryo to the uterine wall is effected. It becomes much thickened and vascularised from the allantoic vessels, and its outer wall becomes phagocytic and in many cases eats its way into the uterine wall, so that the embryo actually becomes imbedded in the

\* In some cases a portion of the foetal tissues remains in the uterus and is absorbed (mole, etc.).

maternal tissues. In the deciduate forms it sometimes grows into the uterine walls round the maternal capillaries, the endothelium of which remains throughout (Carnivora), or disappears (Chiroptera) so that the maternal blood is actually in contact with the foetal tissues in lacunae of the trophoblast. In other cases it develops lacunae which become filled with blood through the rupture of the maternal vessels.

In many lower Mammalia (Marsupialia, Rodentia, etc.) the walls of the sac which corresponds with the yolk-sac of birds develops an area vasculosa which plays an important part in the nutrition of the embryo.

The early development of the mammalian embryo is frequently rendered apparently abnormal by the precocious formation of that part of the trophoblast and adjacent mesoblast which plays later on an important part in the formation of the placenta. This is notably the case in *Homo* and his allies, and in those forms which display the so-called inversion of the layers.

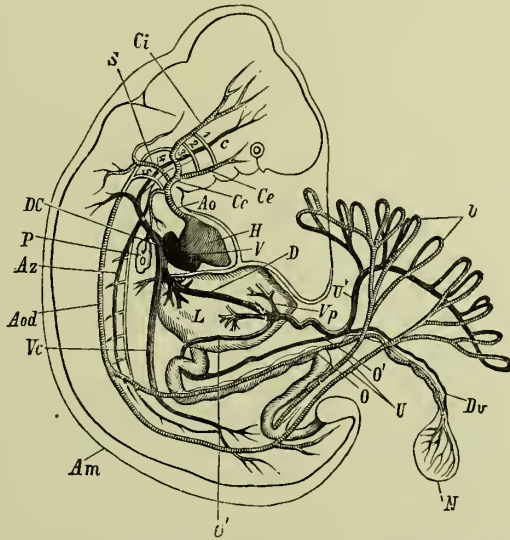


FIG. 272.—Diagram of the arrangement of the principal vessels in a human foetus (after Huxley). *Am* amnion; *Ao* aortic trunk; *Aod* descending aorta; *Az* azygos vein; *C* anterior cardinal vein; *Ce* common carotid; *Ce* external carotid; *Ci* internal carotid; *D* ductus venosus Arantii; *DC* ductus cuvieri; *Dv* vitelline duct (ductus omphalomeseraicus); *H* ventricle; *L* liver; *N* umbilical vesicle (yolk-sac); *O* omphalomeseraic (vitelline) artery; *O* omphalomeseraic (vitelline) vein; *P* lungs; *S* subclavian artery; *U* umbilical (allantoic) arteries with their placental ramifications (*U'*); *U'* umbilical (allantoic) vein; *V* auricle; *Vc* vena cava inferior; *Vp* portal vein; 1, 2, 3, 4, 5 the arterial arches—the persistent aortic arch is not visible.

In the foetus, respiration is effected through the placenta and the lungs are functionless. In correspondence with this the circulation of the foetus differs from that of the animal after birth (Fig. 272). From the heart the blood is driven into the descending aorta, which sends off behind two large vessels to the placenta (umbilical or allantoic arteries). The blood, returning from the placenta in the allantoic vein, passes in great part through a connecting vessel (ductus venosus Arantii) into the

inferior vena cava, and thence in part passes into the right auricle, but the greater part passes, in consequence of a special arrangement of valves, directly into the left auricle through an opening in the interauricular septum, called the foramen ovale. The blood which reaches the right ventricle passes through a vessel (ductus arteriosus Botalli), connecting the pulmonary artery with the aorta, directly into the systemic circulation, except a small portion which goes to the lungs. From this condition of the circulation, it results that all the arterial vessels contain mixed blood. The allantoic vein alone contains pure arterial blood.

As remains of the first stage of the circulation before the development of the placenta, the omphalomeseraic (vitelline) vessels—an artery and a vein—which belong to the umbilical vesicle (yolk-sac), still persist.

The duration of gestation depends on the size of the body and the stage of development at which the young are born. It is longest in the large terrestrial and the colossal aquatic animals (Ungulata, Cetacea), which live under favourable conditions of nourishment. The young of these animals are so far advanced in their bodily development at birth, that they are able to follow the mother (to a certain extent like *præcoces*). The period of gestation is relatively shorter in the Carnivora, the young of which are born naked and with closed eyes and, like *altrices*, are for a long time completely helpless, and need the care and protection of the mother. It is, however, shortest in the aplacental monotremes and marsupials. In these animals the young, which are born at a very early stage (in the kangaroo they are no larger than a nut), pass into a pouch formed by cutaneous folds in the inguinal region, and here adhere firmly to the nipples of the mammary glands. In this pouch, as in a second uterus, they are nourished by the secretion of the mammary glands, which assume at this early stage the nutrient function of the absent placenta. The number of the young, which are born, also varies very greatly in the different genera. The large Mammalia, of which the period of gestation is longer than six months, as a rule bear only one, more rarely two young; but in the smaller Mammalia and some domestic animals (pig) the number is considerably larger, so that twelve to sixteen, or even twenty young may be born at one time. The number of teats on

the mother usually indicates the greater or smaller number of the progeny.

Many Mammalia live a solitary life, and pair only at breeding time ; they are principally such carnivorous animals as find their subsistence by hunting in definite hunting grounds, like the mole in its subterranean passages. Others live united in companies, in which the oldest and strongest males frequently undertake the protection and leadership. Most mammals seek their food by day. Some, e.g. the bat, leave their hiding places in the twilight and at night. Most Carnivora and numerous Ungulata also sleep in the daytime. Some Rodentia, Insectivora, and Carnivora fall, during the cold season of the year when food is scarce, into an interrupted (bear, badger, bat) or continuous (dormouse, hedgehog, marmots) winter sleep in their hiding places, which are often carefully protected, or in nests formed in the earth. During this time the temperature is lowered, the respiration is less active, the heart beat is slowed, and they take up no food, but consume the fat masses which were stored up in the autumn. The following animals are known to migrate : the reindeer, the South African antelopes, and the North American buffalo ; the seals, whales, and bats, but more especially the lemmings, which migrate in enormous herds from the northern mountains southwards to the plains, are stopped by no obstacles on their journey, and even cross rivers and arms of the sea.

The intellectual faculties are more highly developed than in any other class of animals. The Mammalia possess the faculty of discrimination and memory ; they form ideas, judgments, and conclusions ; they exhibit affection and love to their benefactors, dislike, hate, and anger to their enemies ; each individual has a definite character. Further, the intellectual faculties of mammals are capable of being developed and improved, but, except in *Homo*, to a relatively small extent on account of the absence of articulate speech. The more docile of them have been chosen by man as domestic animals, and in this capacity have played an important and indispensable part in the history of civilisation (dog, horse). Instinct always occupies an important place in their life. It leads many of them to construct spacious passages and ingenious nests above or below the earth, in which they rest and bring up their offspring. Almost



all make special nests for their brood, which they often line with soft materials; some even construct true nests, like those of birds, of grass and stalks. Many of those which inhabit subterranean holes and passages store up winter provisions, which they consume in the sterile season, or in autumn and spring (winter-sleepers).

**Geographical distribution.\*** Some orders, as the rodents and bats, are represented in all parts of the world. Of the Cetacea and Pinnipedia most species belong to the polar regions. In general, the Old and New Worlds have each their own fauna. The mammalian fauna of Australia consists almost exclusively of marsupials. The oldest fossil remains (lower jaw) of mammals are found in the Trias (Keuper Sandstone and Oolite, Stonesfield slate) and are supposed to belong to the Marsupialia (p. 539). But it is not until the Tertiary period that the mammalian fauna presents a rich development.

The classification of Mammalia adopted in this work is as follows :—

- Order 1. **Monotremata.**
- „ 2. **Marsupialia.**
  - Sub-order 1. Diprotodonta.
  - „ 2. Polyprotodonta.
  - „ 3. Allotheria.†
- „ 3. **Edentata.**
  - Sub-order 1. Xenarthra.
  - „ 2. Gravigrada.†
  - „ 3. Nomarthra.
- „ 4. **Sirenia.**
- „ 5. **Cetacea.**
  - Sub-order 1. Mystacoceti.
  - „ 2. Odontoceti.
  - „ 3. Zeuglodonta.†
- „ 6. **Hyracoidea.**
- „ 7. **Proboscidea.**
- „ 8. **Ungulata.**
  - Sub-order 1. Artiodactyla.
  - „ 2. Perissodactyla.
  - „ 3. Lipoterna.
- „ 9. **Amblypoda.†**
- „ 10. **Toxodontia.†**
- „ 11. **Typotheria.†**
- „ 12. **Tillodontia.†**
- „ 13. **Ancylopoda.†**
- „ 14. **Condylarthra.†**
- „ 15. **Creodonta.**

\* Wallace, Slater, Lydekker, *op. cit.* † Extinct.

- Order 16. **Carnivora.**
- .. 17. **Pinnipedia.**
- .. 18. **Rodentia.**
- .. 19. **Insectivora.**
- .. 20. **Chiroptera.**
- .. 21. **Prosimiae.**
- .. 22. **Primates.**

There are about 2,300 living and over 3,000 extinct species of mammalia known at the present time. Many of the extinct groups are very imperfectly known, and it seems advisable in the present state of knowledge to give some of these the rank of orders.

### Order 1. **MONOTREMATA.\***

(Sometimes called *Ornithodelphia* and *Prototheria*.)

*Oviparous Mammalia with meroblastic ova.*

The monotremes differ from all other mammals in possessing the following characters, some of which may be described as reptilian. The mammary glands are without teats, and the brain is without a corpus callosum. The pectoral girdle has a large coracoid which reaches the sternum, and a precoracoid. There is also a large T-shaped interclavicle. The vertebrae are without epiphyses, and the ribs are provided only with a capitulum. Marsupial bones are present. The right auriculo-ventricular valve is incomplete and partly muscular. The testes retain their abdominal position. The ureters do not open into the bladder but into a urinogenital sinus, which communicates with the alimentary canal, so that there is a cloaca. The eggs are large and meroblastic, and are laid at an early stage of development. They are however undoubtedly mammals, being provided with hairs, warm blood, non-nucleated red blood-corpuscles and a left aortic arch.

There are but three living genera, and very few fossils are known. The living forms are confined to Australia, Tasmania, and New Guinea.

The form of the body and the mode of life partly recall the anteaters and hedgehog (*Echidna*, Fig. 273) and partly the

\* "Monotremen u. Marsupialen" in *Semon's Zoologische Forschungsreise in Australien*, etc. Bd. 2, 1897. R. Owen, "Monotremata" in *Todd's Encyclopaedia of Anatomy and Physiology*, 1847. W. H. Caldwell. The Embryology of Monotremata and Marsupialia, *Phil. Trans.* 178, 1887, p. 463.

otters and moles (*Ornithorhynchus*, Fig 274); in fact *Ornithorhynchus* received the appropriate name of "watermole" from the Australian settlers. *Echidna* is covered with strong spines, and possesses an elongated edentulous snout, with a vermiform protrusible tongue. The short five-toed legs end with powerful scratching claws, which are adapted for rapid burrowing. *Ornithorhynchus*, on the contrary, has a close soft fur, a flattened body and, as in the beavers, a flat tail. The

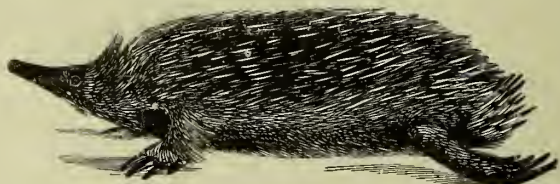


FIG. 273.—*Echidna hystrix*.

jaws, like the beak of a duck, are adapted for burrowing in mud, but are covered by a soft integument which projects at the base of the beak so as to form a kind of shield. The legs are short, with five toes furnished with strong claws and very extensible webs: they are equally well adapted for swimming and burrowing.



FIG. 274.—*Ornithorhynchus paradoxus*.

They lay eggs, with a white membranous shell; *Echidna* deposits them in its pouch; and *Ornithorhynchus*, which has no pouch, is believed, though this has not been absolutely proved, to lay them in its nest.

That the Monotremata are oviparous was suggested soon after their discovery, and has been asserted several times since (on one occasion with good reason), but the best authorities regarded them as viviparous, or at least ovoviviparous, until Caldwell in 1884 definitely settled the matter in the case of *Echidna* by obtaining a specimen with an egg in the pouch. He also found the eggshells of *Ornithorhynchus* in the nest.

The **mammary glands** consist of two groups of glandular tubes which open in a tuft of hairs on two, slightly less hairy, patches of the skin of the abdomen, by numerous openings. The gland-tubes are of the sudoriparous type, being dichotomously branched and provided with smooth muscular fibres outside their epithelium. In *Echidna*, but not in *Ornithorhynchus*, these mammary areas are at the breeding season slightly depressed and placed on the side walls of a forwardly opening pouch of the ventral integument. The egg is placed by the mother in this pouch, where it is hatched and undergoes its early development. The pouch and the depression of the mammary area disappear when the breeding season is over. In *Ornithorhynchus* there is no pouch and no depression of the mammary area (for oviposition see p. 526). In the absence of teats it would appear that the young take up the mammary secretion by licking the mammary area.

The ear is without a pinna. The males possess on the inner side of the hind leg a horny spur, which is attached to an accessory ossicle on the tibial side of the tarsus. This spur is perforated, and transmits the duct of a gland placed beneath the skin of the back of the thigh. The use of this apparatus is not understood, but it is suspected that the gland secretes a poisonous fluid and that the spur is used in fighting, though this has been denied. The young female possesses a small spur which however disappears in the adult.

In the skeleton the following points may be noticed in addition to those already mentioned. The skull-cavity is large, and the cranial walls thin and smooth. The sutures between the bones are largely obliterated. The tympanic bone is annular and slender, and does not form a bulla. The malleus is large, but the incus is small; the stapes is imperforate and columelliform. The mandible is slender and with but slightly marked coronoid process. The odontoid process long remains separate from the axis, and the cervical ribs remain distinct for some time. In the scapula the spine is placed on the anterior border and not in the middle of the bone. In the pelvic girdle of *Echidna* the acetabulum is perforated. The cerebrum is a fair size, and is convoluted in *Echidna*, smooth in *Ornithorhynchus*. There is a large anterior commissure, but no corpus callosum. The cochlea\* is only slightly bent, and alone amongst mammals possesses a lagena with its papilla acustica. *Echidna* is edentulous, but *Ornithorhynchus* possess ten or twelve multituberculate molar teeth.† These are shed at a certain age (half-growth), being ejected and replaced by horny teeth developed beneath them from the epidermal lining of the mouth. The right auriculo-ventricular valve‡ is deficient on the septal side, and there are no chordae tendineae, the papillary muscles being attached to the edge of the valve (the left valve is also without chordae tendineae). In *Ornithorhynchus* (not in *Echidna*) the muscular tissue invades the membranous valve, and the muscular bands are inserted directly into the margin of the opening, so that the valve is partly fleshy. There is in *Echidna* an anterior abdominal vein§ arising on the bladder and distributed to the liver.

The testes are in the abdomen, immediately behind the kidney, to which they are suspended by a fold of peritoneum. There is a urino-

\* Pritchard, *Phil. Trans.*, 1881.

† Poulton, *Q.J.M.S.*, 29. Stewart, *Q.J.M.S.*, 33, 1892, p. 229.

‡ Lankester, *P.Z.S.*, 1883, p. 8.

§ Beddard, *P.Z.S.*, 1884.

genital sinus which posteriorly opens into the cloaca. Anteriorly it receives the openings of the bladder, vasa deferentia and ureters. There is a penis attached to the ventral wall of the cloaca and retractile into a sheath (Fig. 275). It is traversed by a canal (penial urethra) which opens in front into the urinogenital sinus, and behind by more than one opening at the end of the penis. There is a pair of large Cowper's glands opening into the canal of the penis. The corpus fibrosum is not cavernous, but there is cavernous tissue round the urethra and in the glans penis. The prostate and vesiculæ seminales are absent. The ovaries are in the same position as the testes, but the right ovary is smaller (never functional in *Ornithorhynchus*, rarely in *Echidna*) than the left (Fig. 270). There is no vagina. The lower ends of the oviducts are dilated into a kind of uterus, and open into the urinogenital sinus in front of the ureter. There

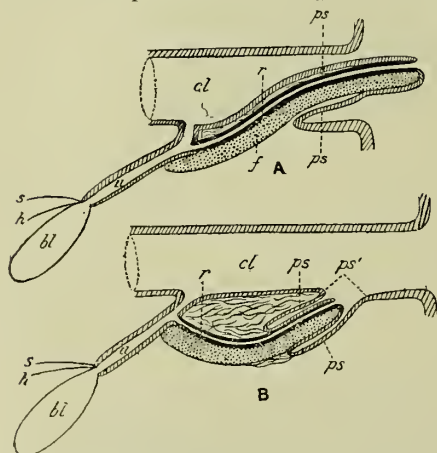


FIG. 275.—Diagram of the cloaca, urinogenital sinus and penis of a Monotreme, A with the penis protruded, B retracted. *bl* connective tissue; *bl* bladder; *cl* cloaca; *f* corpus fibrosum; *p* ureter; *ps* sheath (preputial) of penis; *ps'* opening of this; *r* canal traversing the penis (sperm tube); *s* vas deferens; *u* urinogenital sinus (after Boas).

are two glands opening into the sheath of the clitoris which are compared by Owen to the Cowper's glands of the male.

The ova when they enter the oviduct are larger than in all other mammals (3 to 4 mm.), and contain a considerable quantity of yolk. They acquire an albuminous coat and a shell in the oviduct, where they undergo their incomplete cleavage and the early stages of development. The ovum increases considerably in size in the oviduct by the intussusception of fluid and is about  $15 \times 12$  mm. when extruded.

In *Echidna* one egg is laid at a time and placed

by the mother in the pouch (p. 526). In *Ornithorhynchus* two eggs appear to be laid and placed in the nest in the burrow.

The temperature \* is lower (about  $28-29^{\circ}$  C.) than is usual in mammals and appears to exhibit considerable variation. *Echidna* hibernates in the cold weather. Fossil remains, closely allied to living forms, have been found in the Pleistocene of Australia, and Ameghino † has ascribed some fossils in the Eocene of Patagonia to this group (*Dideilotherium*, etc).

¶ Fam. 1. **Echidnidae**. Skin covered with spines with which hairs are mingled; snout elongated; edentulous; tongue long and protractile; salivary glands large; tail very short. They burrow in sand and earth. *Echidna* Cuv. (1798), with 5 clawed digits on each limb, with a temporary

\* Martin, Thermal adjustment and respiratory exchange in Monotremes and Marsupials, *Phil. Trans.*, 195, 1903, p. 1.

† *Bol. Acad. Cordoba*, xiii, 1894.



pouch in which the single egg is placed, Australia, Tasmania, N. Guinea; *E. aculeata* Shaw. *Proechidna* Gervais (1877), New Guinea, usually with three clawed digits on each limb and traces of the other digits.

Fam. 2. **Ornithorhynchidae.** Covered with a dense soft fur; with the facial portion of the snout broad and elongated and covered with a leathery skin produced into a fold at the base of the snout; with horny molar teeth in old specimens and true teeth up to half growth (p. 527); feet webbed, with 5 clawed toes, the web on the fore foot extending beyond the claws; they are aquatic in habit, and form burrows in the banks of streams, with two openings, one above and one below the water; they are believed to lay two eggs in a nest in the burrow. Australia and Tasmania. *Ornithorhynchus* Blumenb. (1800), water mole, duck-billed Platypus; *O. anatinus* Shaw.

## Order 2. MARSUPIALIA.\*

(Sometimes called *Metatheria* or *Didelphia*.)

*Mammalia with various dentition and epipubic (marsupial) bones. The mammary glands have teats which are usually enclosed in a marsupial pouch in which the young are carried. An allantoic placenta is usually absent.*

The principal characteristic of the Marsupials is the possession by most of them of a sac or pouch (*marsupium*) which is supported by two epipubic (marsupial) bones (Fig. 276), encloses the teats of the mammary glands, and receives the helpless young at birth. Birth takes place at an early stage of development. Even in *Macropus giganteus*, the males of which attain almost the height of a man, the period of gestation does not last more than thirty-nine days, and the embryo at birth is blind and naked, and not much more than an inch in length. It is placed in the pouch by the mother, sucks firmly on to one of the teats, and remains in the pouch for a considerable period.

As additional characters may be mentioned the double vagina, the position of the scrotum in front of the penis, the inclusion of the anus and of the opening of the urinogenital sinus by a common sphincter, the vacuities in the palate, the participation of the alisphenoid in the tympanic bulla, the inflection of the angle of the lower jaw, the absence of the corpus callosum, the absence of a fossa ovalis from the auricular

\* Owen, "Marsupialia," in *Todd's Encyclopaedia of Anat. and Physiol.* 1847. Waterhouse, *Natural History of Mammalia*, 1, London, 1846. Oldfield Thomas, *British Museum Catalogue of Marsupialia and Monotremata*, London, 1888. R. Lydekker, *Handbook to the Marsupialia and Monotremata*, in Allen's "Naturalists' Library," 1894. Bensley, Evolution of the Australian Marsupialia, etc., *Trans. Lin. Soc.* (2), 9, p. 83.

septum and, except in *Perameles*, of an allantoic placenta. As a rule only one tooth (the last premolar) is replaced; the glans penis is generally bifurcated, and the crura penis are not united to the ischia.

The odontoid process fuses early with the axis, and the cervical ribs with their respective vertebrae. There are usually nineteen dorso-lumbar vertebrae of which the anterior thirteen bear ribs. The sacrum consists of two vertebrae, but it may be reinforced by caudal vertebrae. The palate has large posterior vacuities. The alisphenoid assists in forming the tympanic bulla. The carotid canal perforates the basisphenoid. The tympanic, periotic and squamosal remain separate. The jugal reaches back to the glenoid cavity and participates in forming it. The angle of the lower jaw is usually inflected (except in *Tarsipes*). The teeth vary in structure according to the mode of life. The usual formula is  $i \begin{smallmatrix} 3 \text{ to } 5 \\ 1 \text{ to } 4 \end{smallmatrix} c \frac{1}{2} p \frac{3}{5} m \frac{1}{4}$ . As may be seen from the formula the number of incisors and molars is larger than in other mammals. The grinders are either secodont, bunodont or lophodont, and canines are often absent in the herbivorous forms. In some mesozoic forms the canines are two-rooted.

The marsupials are peculiar in the fact that only one tooth—the last premolar—is replaced. In some forms this tooth remains until the animal is full-grown (e.g. *Potorous*); in others (e.g. *Thylacinus*) it is reduced and is absorbed or shed before the other teeth appear. In others again it has not been detected at all, and there is no replacement (*Wombat*, *Dasyurus*, *Myrmecobius*). In the extinct *Sparassodontidae* two premolars and the canines are replaced. Various answers have been given to the question whether the teeth belong to the permanent or milk dentition (see Table on p. 508). By some it is held that all the teeth belong to the milk series, except the tooth which replaces the last premolar, which is regarded as belonging to the permanent series.\* According to this the permanent series must be supposed to have become abortive, a view which is supported by the fact that tooth germs not attaining full development are formed in the position of the permanent tooth germs of the completely diphyodont mammals. However this may be, there is undoubtedly a set of tooth germs which are developed before those of the persistent teeth. These have been called by the upholders of the above-mentioned view prelacteal. Others hold that the deciduous tooth and the persisting teeth belong to the permanent dentition, and that the deciduous tooth is the first of the molar series which in consequence of the shortening of the jaw has been overlapped by the fourth premolar which pushes it out (Tims).

The coracoid is reduced to a process of the scapula, as in the higher forms. A clavicle is present except in the Peramelidae. There is no interclavicle. The bones of the forearm are separate and generally adapted for pronation and supination. The thumb is not opposable, but the two inner digits of the manus can frequently be opposed to the three outer in grasping. The manus possesses five digits except in *Choeoropus*, and the carpus is without an os centrale. Epipubic bones (Fig. 276, *M*) project forwards from the pubis in all except *Thylacinus* in which

\* By some even this is regarded as belonging to the milk series (between the last and penultimate premolar), and arising late (*M. Woodward*, *P.Z.S.*, 1893, p. 467).

they are represented by cartilage. The fibula is generally free, and can sometimes be rotated on the tibia (*Phascolomyidae*, *Didelphyidae*, *Phalangeridae*), and in some cases the first digit can be used as a thumb. The pes presents considerable variation; the tarsus contains the usual seven bones, and there are usually five digits, but the hallux is frequently absent. The second and third digits are in many families very slender, and united by the skin almost to their extremities (*syndactylism*, Fig. 280).

The brain is relatively smaller than in higher mammals. The corpus callosum is absent and the anterior commissure is large. The cerebral

hemispheres vary in size and in the extent to which their surface is convoluted.

The stomach is usually simple, but in the kangaroos it is much elongated and sacculated, like the colon, by three longitudinal muscular bands. There is a cardiac gland in some forms (*Phascolarctus*, *Phascolumys*). The caecum is usually present: it is large in the kangaroos, small and provided with a vermiform appendix in the wombat, absent in the dasyures. A gall bladder is always present.

The heart is without fossa ovalis, the auriculo-ventricular valves are membranous and attached to the papillary muscles by chordae tendineae, and there are two superior venae cavae, each receiving an azygos vein.

**Generative organs.** In the male there are no vesiculæ seminales, the glans penis is frequently bifurcated, the crura penis are not attached to

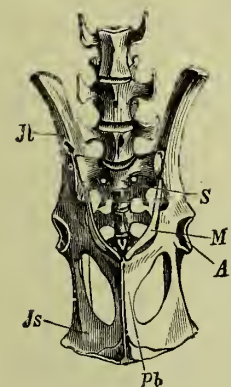


FIG. 276.—The pelvis and adjoining parts of the vertebral column of *Macropus*. *Jl* ilium; *Pb* pubis; *Js* ischium; *M* epipubic bones; *A* acetabulum; *S* the two sacral vertebrae.



FIG. 277.—Bifid penis of *Didelphys phillander* (after Otto, from Gegenbaur). *E* the two halves of the glans.

the ischia, and the testes descend into scrotal sacs which are placed in front of the penis.

In the female\* the müllerian ducts remain separate posteriorly and open separately into the long urinogenital sinus (Fig. 278.) They are differentiated into oviduct, uterus and vagina on each side, and the vaginal portion is curved. This is the arrangement in the simplest cases (*Didelphys*, Fig. 278 *A*), but in other forms the anterior part of the vagina gives off a backwardly directed caecum (Fig. 278 *B*), which is so closely applied to its fellow that it is separated from it only by a median septum. In yet other forms this septum breaks down so that the two vaginal caeca unite into one, the hind end of which reaches back to the front end of the urinogenital sinus. In some forms (*Macropodidae* and others) the hind end of this blind sac acquires at parturition, an opening into the urinogenital sinus at this point (apparently by rupture), so that the foetus is delivered straight into the urinogenital sinus without traversing the whole length of the vagina (Fig. 278 *C*).

\* Brass, A., *Beitr. zur Kenntniss des weibl. Urogenital-system der Marsupialier*, Inaug. Dissert., Leipzig, 1880. Lister and Fletcher, *P.Z.S.*, 1881, p. 976.

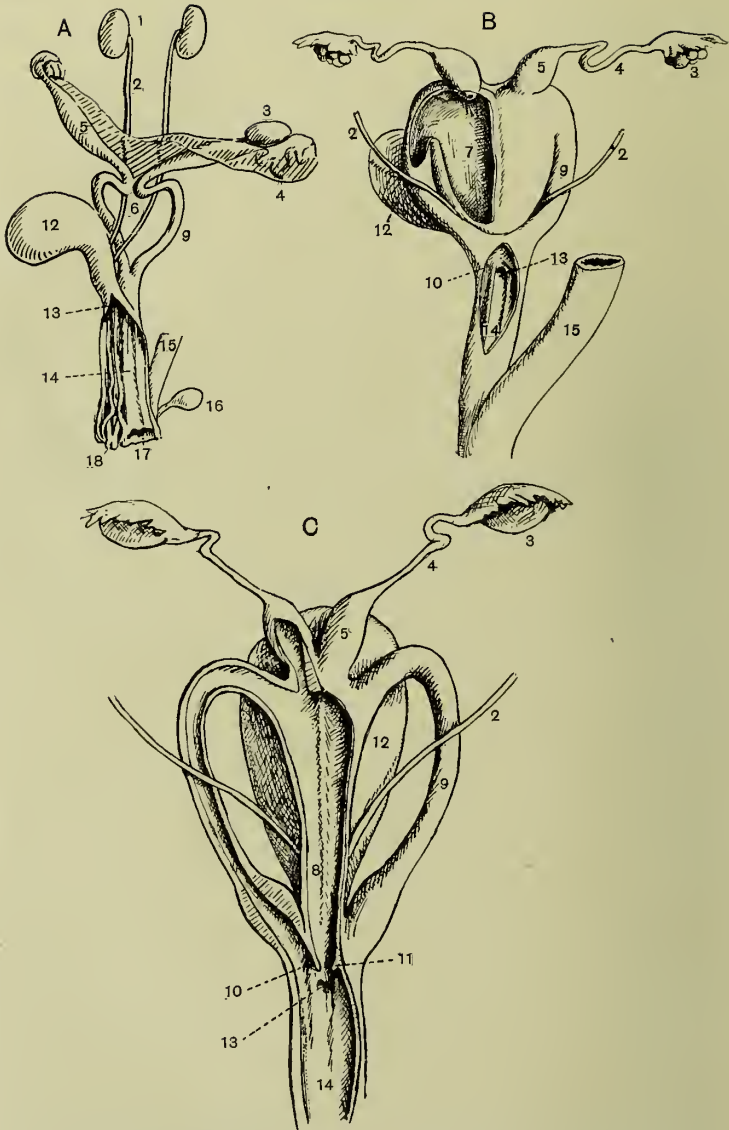


FIG. 278.—Female urinogenital organs, A, a young *Didelphys dorsigera* (after [Brass], ventro-lateral view, the urinogenital sinus is opened. B, *Phalangista vulpina*, dorsal view, the urinogenital canal and left vaginal pouch are opened. C, *Macropus rufus*, dorsal view, the left uterus and vagina, the vaginal pouch or caecum, and the urinogenital canal are laid open; the two vaginal caeca have united and open directly into the urinogenital canal, showing that the animal from which the preparation was made had borne young. (B and C from original drawings by J. J. Lister.) 1, Kidney; 2 ureter; 3 ovary; 4 fallopian tube; 5 uterus; 6 curve where the vagina passes into the uterus; 7 vaginal caecum; 8 vaginal caecum united with its fellow and opening into urinogenital canal; 9 vagina; 10 opening of vagina into urinogenital canal; 11 opening of coalesced vaginal caeca into urinogenital canal; 12 bladder; 13 opening of bladder 14 urinogenital canal; 15 rectum; 16 rectal gland; 17 opening of rectum; 18 clitoris.



In both the male and female the openings of the urinogenital sinus and anus are enclosed by a common sphincter, so that there is a shallow cloaca. In the male this sphincter is said, by compressing the veins of the penis, to exercise an important influence on its erection.

A marsupial pouch is present in most forms. It is however absent in *Didelphys* and the *Dasyuridae*. Its opening generally looks forward, but in *Thylacinus* and some Peramelidae it is directed backwards. The number of teats bears a relation to the number of young produced at a birth. The kangaroo, with one young, has four nipples. The Virginian opossum with several young has six on each side and one in the middle. In *Phascogale penicillata* there are eight nipples arranged in a circle. The young are carried in the mouth to the pouch and are attached by their mouths to the nipples. The nipples are long and the milk is forced down the mouth of the very imperfect young by the contraction of the cremaster muscle. The epiglottis and arytenoid cartilages are elongated and project into the posterior nares in very much the same fashion as in whales. In this way the young are able to breathe while milk is being forced down their throats. In the pouched forms the young return to the pouch for nutrition and shelter after they have acquired the power of locomotion. A rudiment of the pouch is occasionally present in the male.

The ripe ovum appears to be of about the same size as that of higher mammals (in *Phascolarctus* 0.17 mm.). The yolk sac becomes in part vascular; its outer epithelium and that of the false amnion become closely applied to the uterine wall. In some cases at least an epithelial attachment\* is formed, but as a rule no closer connection is established. The majority of the marsupials are therefore truly aplacental, but in *Perameles*† a definite discoidal (primary) allantoic placenta is developed. The young of *Perameles* at birth do not differ in degree of development to any marked extent from other marsupials.

In their external appearance, in their mode of nourishment, and in their habits, marsupials differ much amongst themselves. Some (e.g. kangaroos) are purely herbivorous and in their dentition approach the rodents and ungulates; others (thylacines and dasyures) are carnivorous; but most of them are omnivorous. In their general appearance and mode of locomotion they repeat a series of types of different mammalian orders. Thus the wombats represent the rodents; the fleet kangaroos, which move by huge bounds, correspond to ruminants. The flying marsupials (*Petaurus*) represent the flying squirrels (*Pteromys*); the climbing phalangiers (*Phalangista*), in their shape and mode of life, recall the lemurs; while others, as the Peramelidae, show a likeness to the shrews (*Soricidae*) and insectivores. Finally the carnivorous marsupials approach in

\* Caldwell, *Q.J.M.S.*, 24, 1884. Selenka, *Studien üb. Entwickl. d. Thiere*, iv, *Das Opossum*; v, *Phalangista u. Hypsiprymnus*, Wiesbaden, 1886-91.

† Hill, *Q.J.M.S.*, 48, 1898, p. 385.



their dentition to the true Carnivora as well as to the Insectivora, which they resemble in the large number of their small incisor teeth and tuberculated molars.

The marsupials are in the main confined to the Australian region, but two families, the Didelphyidae and Epanorthidae (*Caenolestes*), are found in the neotropical region to which they are peculiar, and the genus *Phalanger* extends into the island of Celebes, where it is represented by two peculiar species.

The group is divided into eight families with about 180 species.

The geological history of the group is interesting. In Australia, which is now its chief home, no fossil remains are found prior to the Pleistocene. In America, in which both divisions are represented by living forms, remains both of polyprotodonts and diprotodonts are found as far back as the Eocene, and in the case of the Epanorthidae in the Upper Cretaceous. Didelphyids are found in the Tertiaries of Europe, and there is a number of fossil forms in the Jurassic Formation of Europe and N. America, which are ascribed to the polyprotodont division (p. 539). Finally there are the Allotheria or, as they are sometimes called, the Multituberculata (p. 541), remains of which are found fossil in the mesozoic rocks of Europe and N. America, and the exact systematic position of which is still very uncertain.

### Sub-order 1. Diprotodontia.

Incisors three above (one in *Phascolomyidae*) and one below (small second and third incisors sometimes present in *Phalangeridae*), the latter long and powerful. Canines usually small, usually absent below. Molars bluntly tuberculate or ridged. With two syndactylous toes except in *Caenolestes*. Herbivorous, rarely insectivorous. Living forms confined to the Australian and neotropical regions, but found fossil in the Pleistocene of Australia and in the Eocene and Upper Cretaceous of Patagonia and N. America.

Fam. 1. **Macropodidae.** Terrestrial, rarely arboreal; hind limbs longer than the fore, progression generally saltatorial; manus with 5 digits; pes syndactylous, with 4 digits, the hallux being absent (except in *Hypsiprymnodon*), fourth toe very large. Tail long, carried horizontally backwards in progression; stomach sacculated; caecum present; pouch opening forwards. Dentition  $i \frac{3}{1} c \frac{0 \text{ or } 1}{0} p \frac{2}{2} m \frac{4}{4}$ ; the milk premolar is long persistent and molariform, the first premolar is shed with

it but not replaced; the milk premolar is shed usually before the fourth molar appears, and all the grinding teeth move forward in the skull with increasing age as in elephants and some sirenians; the lower incisors are long, and can be used against one another in a scissor-like manner. More than 60 species distributed all over the Australian region.

Sub-fam. 1. **Macropodinae**. With long hairy tail, without hallux; with minute or absent canine. *Macropus* Shaw (*Halmaturus*), kangaroos and wallabies, about 23 species, varying in size from that of a rabbit to that of man, Australia, N. Guinea, E. half of Austro-Malaya; *M. giganteus* Zimm., Australia, except the extreme north, and Tasmania. *Petrogale* Gray, rock-wallabies, Australia, but not Tasmania, 6 species. *Onychogale* Gray, nail-tailed wallabies, with horny excrescence at tip of tail, Australia, not Tasmania. *Lagorchestes* Gould, hare-wallabies, Australia, not Tasmania, 3 species. *Dorcopsis* Schleg. and Müll., 3 species, N. Guinea. *Dendrolagus* Schleg. and Müll., tree kangaroos, arboreal, hardly macropodiform, N. Guinea and North Queensland, 5 species. *Lagostrophus* Thomas, 1 species, W. Australia. Extinct genera, *Palorchestes* Ow., *Sthenurus* Ow., *Synaptodus* de Vis; Pleistocene, Australia.

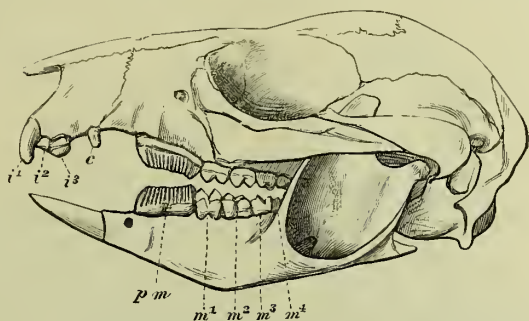


FIG. 279.—Skull and teeth of *Bettongia lesueuri*. c canine; i incisors; pm premolar; m molars (from Flower and Lydekker).

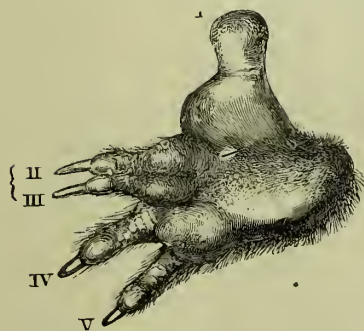


FIG. 280.—*Phalanger celebensis*. Pes showing syndactyly (from O. Thomas).

Sub-fam. 2. **Potoroinae**. Rat-kangaroos, with long hairy tail, without hallux; with canines, generally well developed; premolars with large compressed crowns, and usually grooved on the inner and outer surfaces\* (Fig. 279); small animals. *Aepyprymnus* Garrod, E. Australia, 1 species. *Bettongia* Gray, Australia and Tasmania, 4 species. *Caloprymnus* Thomas, S. Australia, 1 species. *Potorous* Desm. (*Hypsiprymnus* Ill.), Aust. and Tasmania, 3 species.

Sub-fam. 3. **Hypsiprymnodontidae**. With naked scaly tail and an opposable hallux; intermediate to *Phalangeridae*; one species

\* As in some of the extinct Allotheria, see p. 541.

[ and genus only. *Hypsiprymnodon* Ramsay, musk-kangaroo, Queensland.

Fam. 2. **Phalangeridae**. Arboreal, sometimes with parachute-like expansions of the skin for flying leaps; 5 fingers and toes, with nailless opposable hallux; pes syndactylous (Fig. 280); tail long and usually prehensile; stomach simple; caecum present except in *Tarsipes*; pouch opening forwards; dentition variable owing to the presence of minute teeth which are not constant, even in the same species or on two sides of the same jaw; general formula  $i \frac{3}{1} c \frac{1}{0} p \frac{2 \text{ to } 3}{0 \text{ to } 2} m \frac{3 \text{ to } 4}{3 \text{ to } 4}$ ; milk

premolar generally small and early deciduous; Papuan Islands, Australia and Tasmania; about 35 species. Flying membranes are present in 3 genera, which are more closely allied to genera without flying membranes than to each other.

Sub-fam. 1.

**Tarsipedinae.**

Tail long; snout long and slender, tongue extensile; without caecum; grinding teeth minute; lower jaw without inflection.

*Tarsipes* G. and V., about the size of a mouse, ex-



FIG. 281.—*Petaurus sciurius*, 'squirrel flying-phalanger (from Flower and Lydekker).

tracts honey from flowers with its tongue, also insectivorous; 1 species.

Sub-fam. 2. **Phalangerinae**. Dentition normal; tail long, generally prehensile; snout broad; tongue not extensile; without cheek pouches; with large caecum; throughout the Australian region. *Acrobates* Desm., with flying membrane, Queensland, N. S. Wales, Victoria; 1 species. *Distoechurus* Peters, New Guinea, 1 species. *Dromicia* Gray, dormouse-like; N. Guinea, W. Australia, Tasmania; 4 species. *Gymnobelideus* McCoy, like *Petaurus* but without flying membrane, Victoria, 1 species. *Petaurus* Shaw (Fig. 281), with flying membrane, medium or small size, fur soft and silky; insecti-

vorous and extracts honey from flowers; Papua and Australia, 3 species. *Dactylopsila* Gray, Papua and N. Australia. *Petauroides* Thomas, with flying membrane, Queensland to Victoria, 1 species. *Pseudochirus* Ogilb., Tasmania, Australia, N. Guinea; about 10 species. *Trichosurus* Less. (Fig. 282), large size, Australia and Tasmania; 2 species. *Phalanger* Storr (*Cuscus*), largish size, Austro-Malaya from Celebes to Queensland, 5 species; *Ph. ursinus* and *celebensis* from Celebes. *Archizorurus*, *Palaeopetaurus*, *Burramys* have been described from the Pleistocene of Australia.

Sub-fam. 3. **Phascolarctinae.** Muzzle short, tongue not extensile; tail absent; caecum large; cheek pouches present. *Phascolarctus* Blainv., the kaola or native bear, S. E. Australia, two feet in length and a good climber, 1 species.

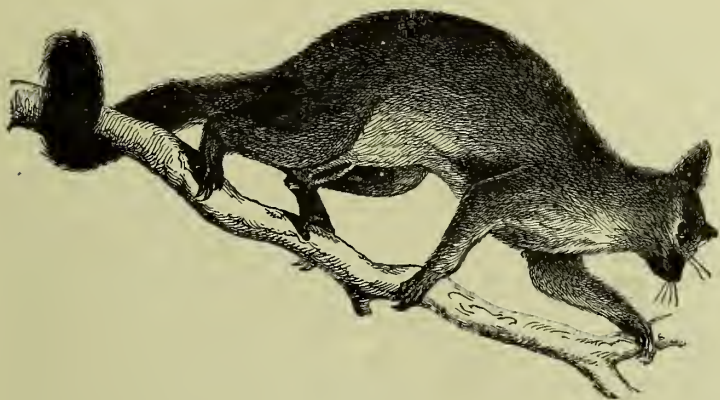


FIG. 282.—*Trichosurus vulpinus* (from Claus).

Sub-fam. 4. **Thylacoleontinae.** Large, extinct forms from the Pleistocene of Australia; dentition  $i \frac{3}{4} c \frac{1}{6} p \frac{3}{4} m \frac{1}{2}$ , last premolar being large and trenchant, like that of the rat-kangaroos. The orbit is completely surrounded by bone, which is not the case in any other marsupial. It was probably a phalanger-like animal, mainly herbivorous, but possibly partly carnivorous. *Thylacoleo* Owen, Pleistocene, Australia.

Fam. 3. **Phascolomyidae.** Fossorial, root-eating forms with stout, clumsy body. Limbs subequal; manus with 5 subequal digits, pes with 4 strong toes and a short nailless hallux, digits 2 and 3 showing a slight tendency towards syndactylism; tail reduced to a stump; stomach simple with cardiac gland; caecum short, with vermiform appendix; pouch present. Dentition  $i \frac{1}{4} c \frac{0}{6} p \frac{1}{4} m \frac{4}{4}$ , all teeth with persistent pulps, incisors rodent-like, with enamel only on front surface, milk premolar not known; Tasmania and S. Australia. *Phascalomys* E. Geoff., wombat, 3 species. Extinct forms from the Pleistocene of Australia are *Phascolonus* Ow., nearly as large as a tapir, *Sceparnodon* Ow.

\* Fam. 4. **Diprotodontidae.** Extinct forms from the Pleistocene of Australia. *Diprotodon* Ow., very large forms of the size of a rhinoceros, resembling *Macropus* but with subequal limbs; palate fully ossified;



humerus without entepicondylar foramen. *Nototherium* Ow., rather smaller than *Diprotodon*.

Fam. 5. **Epanorthidae**. American Diprotodonts, without syndactylism; mostly extinct. The only living genus *Caenolestes* Thomas (*Hyracodon*) with small vestigial pouch and dentition  $i \frac{4}{3}$   $c \frac{1}{1}$   $p \frac{3}{3}$   $m \frac{4}{4}$ ; mountains of Ecuador and Colombia, 2 species, several extinct genera from the Eocene of Patagonia. *Cimolestes*, *Telacodon* and *Batodon* are also found in the Upper Cretaceous of N. America, and *Epanorthus* in the Upper Cretaceous and Eocene of Patagonia. The extinct **Abderitidae** and **Garzonidae** from the Eocene of Patagonia also come here.

## Sub-order 2. Polyprotodontia.

Incisors numerous, sub-equal, four or five above and three or four below; canines large, molars cuspidate. Without syndactylism except in the *Peramelidae*. Mostly carnivorous and insectivorous. America and Australia.

Fam. 1. **Peramelidae**. Bandicoots. Fossorial, insectivorous, hind legs longer than fore, with syndactylism of digits 2 and 3 of the pes. Manus with 2 or 3 of the middle digits long and functional, the others small or absent; pes with 4 or 5 digits, unequal in size, digits 2 and 3 slender, united; hallux small or absent. Stomach simple, caecum present, pouch opening backwards. Dentition  $i \frac{4 \text{ or } 5}{3}$   $c \frac{1}{1}$   $p \frac{3}{3}$   $m \frac{4}{4}$ . Australia and Papua. *Peragale* Gray, rabbit-bandicoots, digits 2, 3 and 4 of manus large, digits 1 and 5 present but small and clawless; hallux absent; ears large; omnivorous; Australia; 2 species. *Perameles* Geoff., fore limbs as in *Peragale*, hallux present, clawless, ears medium; embryo with placenta (p. 533); Australia, Tasmania and N. Guinea. *Choeropus* Ogilb., pig-footed bandicoots, fore-limbs with digits 2 and 3 only functional, digit 4 small, digits 1 and 5 absent; hallux absent; ears long; omnivorous, Australia, 1 species.

Fam. 2. **Dasyuridae**. Predatory, carnivorous or insectivorous, with subequal limbs, usually pentadactyle, but hallux sometimes absent; no caecum; pouch present or absent, opening forwards or downwards. Dentition  $i \frac{4}{3}$   $c \frac{1}{1}$   $p \frac{2 \text{ or } 3}{2 \text{ or } 3}$   $m \frac{4 \text{ or } 5}{4 \text{ to } 6}$ ; canines large, molars cusped, milk tooth minute, shed during infancy; Papua and Australia. *Thylacinus* Temm., Tasmanian wolf, size and build of a wolf, back transversely banded with black, hallux absent, dentition  $i \frac{4}{3}$   $c \frac{1}{1}$   $p \frac{3}{3}$   $m \frac{4}{4}$ , Tasmania (fossil in N. S. Wales), 1 species. *Sarcophilus* F. Cuv. (*Diabolus*), Tasmanian devil, about the size of a badger, body powerful, blotched with white, hallux absent, dentition  $i \frac{4}{3}$   $c \frac{1}{1}$   $p \frac{2}{2}$   $m \frac{4}{4}$ , milk premolar, reduced, and absorbed or shed before the other teeth cut the gums; Tasmania (fossil in N. S. Wales), 1 species. *Dasyurus* E. Geoff., native cats, body viverrine, profusely spotted with white, hallux sometimes present, dentition as in the last, but more insectivorous; Papuan and Australian regions, 5 species, feed on birds and eggs, nocturnal. *Phascogale* Temm., small, not larger than a rat, hallux present, dentition  $i \frac{4}{3}$   $c \frac{1}{1}$   $p \frac{3}{3}$   $m \frac{4}{4}$ , arboreal, insectivorous; pouch absent, represented by fold of skin;



Papuan and Australian regions, 13 species. *Sminthopsis* Thomas, small forms with hallux and pouch, Australia and Tasmania, 4 species. *Antechinomys* Krefft, jerboa-like, terrestrial, without hallux, Queensland and N. S. Wales. *Myrmecobius* Waterh., arboreal and terrestrial, anteaters, red and squirrel-like, tongue long, extensible; lower lip pointed; back banded with white, hallux absent, molars and premolars exceeding the usual number of 7; dentition  $i \frac{4}{3} c \frac{1}{1} p \frac{3}{3} m \frac{5}{5 \text{ or } 6}$ , without pouch, allied by its dentition to the Jurassic polyprotodont marsupials, W. and S. Australia, 1 species.

Fam. 3. **Notoryctidae**,\* mole-marsupial, red colour, mole-like form and habits, without externally visible eyes or ears, pentadactyle limbs, upper molars tritubercular, pouch opening backwards, central South Australia, one genus and species. *Notoryctes* Stirling.

Fam. 4. **Didelphyidae**. Opossums, arboreal (except *Chironectes minimus* which is aquatic), carnivorous or insectivorous, pentadactyle forms with an opposable hallux for climbing. Tail long, prehensile; stomach simple; caecum small or moderate; dentition  $i \frac{5}{4} c \frac{1}{1} p \frac{3}{3} m \frac{4}{4}$ ; pouch generally absent, sometimes represented by two folds of skin, N. and S. America, fossil in Eocene, Oligocene and Miocene of Europe and America; two genera. *Didelphys* L., hind toes free, size from that of a cat to a large mouse, with 23 species (this genus has been divided into a number of sub-genera, *Didelphys*, *Metachirus*, *Philander*, *Micoureus*, *Peramys*). *Chironectes* Ill., water opossum, hind toes webbed to their extremities, about the size of a rat, Guatemala to S. Brazil, 1 species. *Amphipraterium* Filhol., from the Oligocene and Miocene of Europe and *Peratherium* from the Eocene and Miocene of Europe and America, and from the Pliocene and Pleistocene of America, belong to this family.

A number of fossil forms known by little more than their lower jaws and teeth and found in Mesozoic rocks, are associated in current classifications with the polyprotodont marsupials. These include the celebrated lower jaws of the Stonesfield Slate (Lower Jurassic) of Oxfordshire and of the Middle Purbeck Beds (U. Jurassic) of Dorsetshire. Apparently similar remains are found in N. America in the U. Jurassic and U. Cretaceous formations, and two forms, viz. *Dromatherium* and *Micronodon* are known by lower jaws in the Upper Trias of Carolina. The reasons for associating these remains, which belonged to quite small animals no larger than a rat, with the marsupials are indeed slender, based as they are only upon the dentition of the lower jaw and upon the fact that in some of them the angle of the mandible is slightly inflected. The dentition resembles that of *Myrmecobius*, and consists of at least three lower incisors, well-developed canines and cuspidate molars and premolars.

These forms have been grouped in families which are here tabulated as an appendix to the *Polyprotodontia*, for convenience of reference and not because any real importance can be attached to the grouping.

Fam. 5. **Dromatheriidae**. Premolars styliform, molars triconodont, with main cusp and several anterior and posterior smaller accessory cusps all in the same line; dentition of mandible  $i 3 c 1 p 3 m 7$ ; from the U. Trias of Carolina; by many regarded as reptiles. *Micronodon* Osborn, *Dromatherium* Emmons.

Fam. 6. **Triconodontidae**. With 4 premolars and 4—8 molars; canines

\* Stirling, *Trans. Roy. Soc. S. Australia*, 1891, p. 154; Gadow, *P.Z.S.*, 1892, p. 361.

often with bifid root; premolars and molars with 3 cusps in a row (triconodont), with a strong cingulum and with bifid roots; angle of mandible inflected. Jurassic of England and N. America. *Triconodon* Owen, Middle Purbeck Beds of Dorsetshire and U. Jurassic of Wyoming. *Amphilestes* \* Owen, Stonesfield Slate. *Phascolotherium* Owen, Stonesfield Slate. *Spalacotherium* Owen, Purbeck, Dorsetshire, lower molars with one large outer cusp and two small inner cusps (tritubercular), resembling those of some Insectivora; dentition of mandible  $i\ 3\ c\ 1\ p\ 4\ m\ 6$ . *Priacodon*, Marsh. etc. U. Jurassic, Wyoming.

Fam. 7. **Amphitheriidae**.† With numerous two- or three-rooted trituberculated lower molars with a heel (so-called tubercular-sectorial, Fig. 283), resembling those of the opossums, bandicoots, some insectivores, and the lower carnassial teeth of Carnivora; the main cusp (inner in the upper jaw, outer in the lower) is connected with the two other cusps by crests; premolars with three cusps in a row and with cingulum; canines usually two-rooted; angle of mandible often slightly inflected. Jurassic and Cretaceous. *Amphitherium* Blv., Stonesfield Slate; the lower jaw upon which this genus is based was together with that of *Phascolotherium*, the first of the remains of Mesozoic Mammalia discovered. The specimens

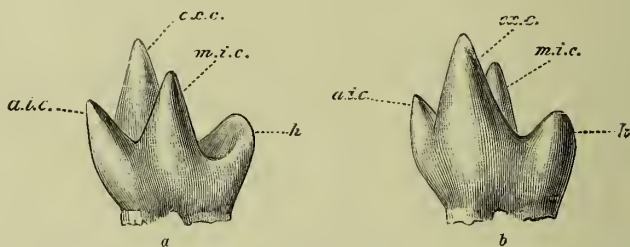


FIG. 283.—a Inner face of a molar of the right ramus of the lower jaw of *Amphitherium prevostii*. b Hypothetical representation of the outer face of the corresponding tooth of the left ramus (after Goodrich). a.i.c. anterior internal cusp (paracone), e.c. external cusp (protocone), h heel, m.i.c. median internal cusp (metacone).

were brought to Mr. W. J. Broderip of Oxford about the year 1814, and one of them was acquired by Professor Buckland and placed in the Ashmolean Museum; it is now in the Oxford University Museum; dentition of lower jaw  $i\ 4\ c\ 1\ p\ 5\ m\ 6$ ; angle of mandible slightly inflected; mylohyoid groove conspicuous. *Peramus* Owen, U. Jurassic of England. *Amblotherium* Owen, Purbeck, *Dryolestes* Marsh, Upper Jurassic and Upper Cretaceous of N. America.

The **Sparassodontidae** (**Borhyaenidae**) present resemblances to the carnivorous marsupials of Australia, and may be placed near the Dasyuridae, which they resemble in their dentition. They are of considerable or moderate size with a dentition of  $i\ \frac{4\ to\ 2}{4\ to\ 0}\ c\ 1\ p\ \frac{3}{4\ to\ 3}\ m\ \frac{4}{4}$ ; the canines (well-developed) and two premolars only are known to have been replaced; the upper molars are tritubercular, the lower cutting; there are no marsupial bones and the characteristic marsupial palatal vacuities are absent; the angle of the mandible is strongly inflected. By

\* Goodrich, *Q.J.M.S.*, 35, 1894, p. 407.

† Goodrich, *op. cit.*

some observers they are placed with the Creodonta, to which they are probably allied. All extinct, in the older Tertiaries of Patagonia. *Borhyaena*, *Prothylacinus*, *Amphiproviverra*, etc., Ameghino.

### Sub-order 3. *Allotheria*.

The *Allotheria* (*Multituberculata*) are sometimes treated as a separate order of the Mammalia, sometimes as a sub-order of the Marsupialia, and sometimes as a sub-order of the Monotremata. The group is known to us by very fragmentary remains, consisting of little more than teeth, sometimes the lower jaw, and in a few cases of parts of the skull and small portions of other parts of the skeleton. They possess multituberculate molars with the tubercles arranged in two or three rows, and the premolars are either similar or provided with a secant obliquely grooved edge, not unlike those of certain Macropodidae. An important feature of the dentition, and one which also recalls the diprotodont marsupials, is the presence of a pair of large rodent-like incisors in the lower jaw and of a pair of large incisors and sometimes of one or two pairs of smaller incisors in the upper jaw. Canines are absent; the lower jaw is without the mylohyoid furrow, and its angle is inflected. In one form remains of the scapula have been found which suggest the presence of a distinct coracoid. They have been found in a bed of marl a few inches thick in the Middle Purbeck (U. Jurassic) of Swanage, in the Jurassic of Wyoming, U.S.A., and in the Laramie beds of the Upper Cretaceous of the same country. *Tritylodon*, if it be a mammal, is from the Trias of Stuttgart and of S. Africa, and *Microlestes* from the Trias of Bavaria. They also extend into the lower Eocene of N. America and France. In the Laramie formation limb-bones have been found which have been ascribed to this group—pelvic bones not united, and a scapula with two facets, one of which is supposed to have been for a coracoid (*Camptomus*).

Fam. 1. **Tritylodontidae**. Premaxilla with a strong canine-like incisor and a smaller incisor behind, upper and lower premolars alike, the latter with three rows of tubercles. Trias of S. Africa and Europe; by many regarded as reptiles. *Tritylodon* Ow., Karoo formation; *Triglyphus* Fraas, Trias of Stuttgart.

Fam. 2. **Bolodontidae**. With two or three pairs of incisors in the upper jaw; upper premolars with three or four cusps. Jurassic, Cretaceous, Tertiaries. *Bolodon* Ow., Purbeck; *Allodon* Marsh, Upper Jurassic Wyoming; *Allacodon* Marsh, Upper Cretaceous.

Fam. 3. **Plagiaulacidae**. Lower jaw with one pair of large rodent-like incisors and inflected angle; three or four cutting premolars marked with oblique ridges on the outer face, and two small molars with tuberculated (crenulated) edges. Trias to Eocene. *Microlestes* Plieninger (*Hypsiprymnopsis* Dawkins), Upper Trias of Somerset and Wurtemberg. *Plagiaulax* Falconer, Purbeck of Dorsetshire. *Ctenacodon* Marsh, U. Jurassic, Wyoming and several genera from the Laramie beds (U. Cretaceous) of N. America. *Ptilodus* Cope, L. Eocene of New Mexico and *Neoplagiaulax* Lemoine, Lower Eocene of France.

Fam. 4. **Polymastodontidae**. Rather larger animals with a pair of rodent-like incisors in the lower jaw, and tuberculated premolars and molars. Lower Eocene of N. America, and teeth in the Laramie beds. *Polymastodon* Cope.

**MONODELPHIA.**(Sometimes called *Eutheria*.)

This group includes the remaining orders of the Mammalia. The urinogenital organs almost always open independently of the rectum, and the vagina is single, though occasionally it is partly divided into two by a median septum. There is no marsupial pouch nor epipubic bones. The embryo is always provided with an allantoic placenta and born at an advanced stage of development. The corpus callosum of the brain is well-developed. The testes usually pass into a scrotal sac, which is always placed at the sides of or behind the penis.

**Order 3. EDENTATA \* (BRUTA).**

*Mammals with incomplete dentition, usually with numerous grinders without roots, and with scratching or curved claws on the extremities. Teeth are always absent from the anterior part of the mouth, and they are without enamel.*

This order, which includes but few genera (sloths, anteaters, armadillos), is characterised by the relatively low grade of development of all the organs, and especially by the incompleteness of the dentition, teeth being in exceptional cases absent altogether. Except in the case of a single dasypod, incisors are always absent. When canines are present they are small, blunt and conical. All the teeth are devoid of enamel, consisting of soft dentine covered externally by hard dentine and sometimes cement, and they grow from persistent pulps (rootless). With the exception of some armadillos (*Tatusia*, etc.) and *Orycteropus*, milk teeth are not formed, and there is no replacement (monophyodont). The ischium is almost always united to the sacrum. The brain is variable; the cerebrum may be smooth and the corpus callosum small, or it may be convoluted and possess a large corpus callosum. The reproductive organs are also variable. The vestibule (urinogenital canal) of the female is long, and the testes almost always remain in the body. There are two superior venae-cavae, and retia mirabilia are often present in the extremities.

\* W. v. Rapp, *Anatomische Unters. über die Edentaten*, Tübingen, 1852. Fl. Ameghino, Sur les Edentés Fossiles de l' Argentine, *Revista del Jard. Zool. de Buenos-Aires*, iii, 1895, p. 113. R. Lydekker, *Ann. Mus. La Plata, Palaeont. Argentina*, iii, 1893. For Bibliography, see Flower and Lydekker's *Mammals Living and Extinct*, 1891.



Most of them are insectivorous (anteaters and armadillos), a few are phytophagous (sloths). Many of them are burrowing animals, but a few are arboreal. At the present day they are confined to Africa, Asia and America. They are first found fossil in the U. Cretaceous of Patagonia (Ameghino), and are supposed to have relations through the *Ganodonta* and *Tillo-dontia* (see below), with the early Carnivora and Rodentia, but this is a highly speculative view.

The *Edentata* may be divided into two main divisions—the *Xenarthra* and the *Nomarthra*. The *Xenarthra* comprise all the American forms, viz., the anteaters (*Vermilinguia*), the sloths (*Tardigrada*) and the armadillos (*Loricata*) with the extinct *Glyptodontidae*. The *Nomarthra* are the Old-World forms, *Orycteropus* and *Manis*. The New-World forms (*Xenarthra*) undoubtedly constitute a natural group, inasmuch as the extinct ground sloths connect the apparently diverse sloths and anteaters. This cannot be said of the Old-World genera *Manis* and *Orycteropus*. It is difficult to see in what fundamental points these show special affinity either to each other or to the *Xenarthra*. There is an immense number of extinct forms belonging to the *Xenarthra*, some of them very remarkable, e.g. the Megatheriidae or ground sloths, and the Glyptodontidae or extinct armadillos. These are all, like their living allies, confined to the New-World.\* They date from the Eocene or U. Cretaceous of S. America.

### Xenarthra.

With additional articulating processes on the posterior dorsal and on the lumbar vertebrae; the scapula has a second spine; the ischia are united to the part of the sacrum formed by the anterior caudal vertebrae; the testes are in the abdomen between the rectum and the bladder, the penis is small, the uterus simple, and the placenta dome-shaped (the chorion being complete). They are exclusively American and mainly S. American, one or two forms extending into the southern part of N. America. *Necrodasypus* Filhol, from the Eocene of France, has been assigned to the *Xenarthra*, but the remains are too incomplete for certainty as to their systematic position.

\* Grandidier (*Bull. Mus. Paris*, 1901, p. 54) has described the remains of a ground sloth, which he calls *Bradytherium*, from Madagascar.



Fam. 1. **Myrmecophagidae**. Antcaters, hairy, edentulous, without tooth-germs; with long snouts, long protrusible tongues, and enormous submaxillary salivary glands. The clavicles are reduced. The anterior margin of the scapula is produced over the coraco-scapula notch to meet the coracoid. In the manus the third digit is greatly developed and provided with a strong claw; the other digits are reduced or suppressed. The pes has four or five subequal digits with claws. The cerebrum is convoluted and has a large corpus callosum and anterior commissure. Uterus simple. Confined to the neotropical region. *Myrmecophaga* L., skull elongated with rostrum composed of mesethmoid, vomer, maxillae, nasals; premaxillae small and confined to the margin of the terminal nares; zygomatic arch incomplete; pterygoid with palatal plates; mandible slender without coronoid. Vertebrae, C7, D15-16, L2-3, S6, C31. Sternal articulation of the ribs double. Manus and pes with 5 digits. The animal walks on the end of digit 5 and on the dorsal sides of digits 3 and 4 of its manus and on the sole of its pes. Stomach with thin-walled cardiac portion, and a thick-walled gizzard-like pyloric; ilio-colic valve absent, caecum short. Two pectoral mammae; produces one at a birth. One species, *M. jubata* L. the great anteater, ant-bear, body 4 feet in length and 2 feet in height at shoulder; with long fur; eats termites which it obtains with its long tongue, having broken into the ant-heap with its strong claws; terrestrial; trop. S. and C. Amer. *Tamandua* Gray, like the last, but smaller, with shorter fur, and tail tapering and scaly at the end; head less elongated, pterygoid with palatal plates. Vertebrae, C7, D17, L2, S5, C37. Manus with 5 digits, the fifth being concealed in the skin, pes with 5 digits; arboreal, forests of S. and C. Amer., 3 species. *Cycloturus* Gray, smaller than the last, about the size of a rat, head short, pterygoid without palatal plates; vertebrae C7, D16, L2, S4, C40. Manus with two complete digits (2 and 3), digit 4 with one nailless phalanx, digits 1 and 5 with metacarpal only; in the pes, the hallux is concealed and has one phalanx, digits 2-5 are subequal; ribs broad, overlapping; clavicle complete; stomach without gizzard-like portion, colon with 2 small caeca; arboreal, one species S. and C. Amer.

Fam. 2. **Bradypodidae (Tardigrada)**. Sloths, vegetable-feeders and arboreal, with long coarse hair, coloured green by a parasitic alga; with rounded head, anteriorly directed eyes, long anterior limbs, short tail, and pectoral mammae. With 5 pairs of teeth in the upper and 4 pairs in the lower jaw, consisting of vaso-dentine covered with cement; without succession. Long bones without medullary cavities. Zygomatic arch incomplete with downwardly directed process (Fig. 284); lower jaw with coronoid; cervical vertebrae unusual in number, dorsals often very numerous. The anterior border of the scapula coalesces with the coracoid, and the acromion is united by cartilage with the coracoid; clavicles present; scaphoid and trapezium united; digits never more than 3, with long curved claws. Stomach complicated, with several chambers; caecum absent; uterus simple and globular, divided by longitudinal partition; testes placed as in *Myrmecophagidae*; penis minute, crura not directly attached to ischia. The sloths are exclusively arboreal; they use the curved claws at the end of the two or three closely connected digits for hanging on to branches during their slow movements; on the ground they move very awkwardly; forests of S. Amer. *Bradypus* L. Three-toed sloths, the ai; no tooth projecting beyond the rest; vertebrae

C9, D15-17, L5-3, S6, C11; manus and pes with 3 digits (2, 3, and 4); with trapezoid and os magnum united; 2 pectoral mammae; trachea folded on itself; several species, but number uncertain, Guiana, Brazil, Peru, Isthmus of Panama. *Choloepus* Ill., two-toed sloths; anterior tooth in each jaw caniniform and separated by diastema from the others; vertebrae C6 or 7, D23-24, L3, S7 or 8, C4-6; manus with 2 digits (2 and 3), pes with 3 digits (2, 3, 4); 2 species; *Ch. didactylus* L., unau. Extinct genera are *Entelops* and *Trematherium* Amegh., Eocene of Patagonia.

A number of extinct families, intermediate between the sloths and anteaters, are united under the heading of **Gravigrada** (ground-sloths). They are for the most part of considerable size, and are found in the Tertiaries of N. and S. America. They date from the Eocene. In their skull and dentition they resemble the sloths, in the vertebral column, limbs and tail the anteaters. The teeth are usually  $\frac{3}{4}$ , and consist of dentine and cement. The anterior border of the scapula is joined to the coracoid process as in the two preceding families, and there is a well-developed clavicle. In some, small bony nodules were present in the skin. The jugal is very strong and has a downwardly directed process. Tail well developed.

Fam. 3. **Megatheriidae**. With very deeply-rooted prismatic teeth, quadrate in section and set in close series. *Megatherium* Cuv., enormous animals with a small head, a body as large as that of an elephant but with shorter limbs; skull sloth-like, zygoma complete with descending process; complete skeletons are known; Pleistocene of S. and C. Amer. and of the southern United States. *Interodon* Amegh., Oligocene, Pliocene of Argentina; *Promegatherium* Amegh., Oligocene, Argentina, with bands of enamel on the teeth; and other genera.

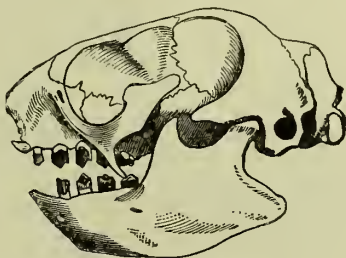


FIG. 234.—Skull of *Bradypus torquatus* (from Claus).

Fam. 4. **Mylodontidae**. With prismatic teeth, sloth-like skull, and jugal reaching back to squamosal but not united to it; skin often with ossifications. *Myodon* Owen, as large as a rhinoceros, dermal bony plates not fused together; Pliocene and Pleistocene of S. Amer. and United States. *Glossotherium* Ow., Pliocene and Pleistocene of Argentina. A portion of the skin of this animal with the hair perfectly preserved was discovered by Moreno in Patagonia in 1897 (*Proc. Zool. Soc.* 1899). A number of scattered small ossicles were embedded in it, and it was assigned to a new genus *Neomyodon*. Later another piece of skin was found by Hauthal in a cave in S. Patagonia in association with some bones of an extinct ground sloth which has since been identified as *Glossotherium* (*Grypotherium*) (*Proc. Zool. Soc.*, 1900, p. 64). A quantity of cut hay and a thick deposit of the excrement of a large herbivore, presumably *Glossotherium*, were also found in the cavern, and Hauthal formed the conclusion that the animal had been kept and fed by man. The bones are in a very fresh state of preservation, retaining their gelatine and showing traces of the dried periosteum and ligaments. There can be little doubt that the skin and bones belonged to the same species of animal

and that the latter was contemporaneous with man, whose remains were also found in the cavern, together with those of an extinct horse and portions of a large feline carnivore. There were also traces of fire in the cavern. *Scelidotherium* Ow., Miocene and Pliocene of Argentina; *Nothrotherium* Lydekker, Pleistocene of Brazil and Argentina *Promylodon* Amegh., Oligocene of Argentina, with bands of enamel on the teeth; and many other genera.

Fam. 5. **Megalonichidae** with several genera, for the most part smaller in size, including *Hapalops*, etc., from the Eocene of S. America; *Nothropus*, from the Pleistocene of Argentina; *Megalonyx*, from the Pleistocene of N. America, and the Antilles.

Fam. 6. **Dasypodidae**.\* Armadilloes. The back and sides of the body are covered by an armour of suturally united bony scutes, over which lie horny epidermal scales. These scutes are usually united into four shields. There is a *cephalic* shield on the head, a *scapular* shield on the shoulders, a *pelvic* shield attached to the ilia and ischia and arching over the rump, and on the trunk a *thoraco-abdominal* shield, which frequently consists of a number of moveable transverse zones, which are connected by soft skin and permit of the body being rolled into a ball. There may also be a *nuchal* shield on the neck. The scapular and pelvic shields overhang the sides of the body and form chambers into which the limbs can be withdrawn. The tail also is more or less completely encased in bony rings, and the outer surfaces of the limbs are protected by irregular scutes. The ventral surface of the body is soft and hairy, and hairs may project between the scales on the back. In *Chlamydomorphus* the bony scutes are strongly developed in the pelvic region only. The dentition is monophyodont except in *Tatusia*; the teeth are numerous and not found in the fore part of the mouth except in one or two forms in which there is one tooth in each premaxilla. Premaxillae well developed; zygoma complete. The atlas is free, but more or fewer of the other cervical vertebrae are ankylosed by their centra and arches as in Cetacea. Lumbar and hinder dorsal vertebrae with accessory articulating processes. The first rib is broad and flattened. The scapula has a second spine in the postscapular fossa. Clavicles well developed. The femur has a third trochanter and the tibia and fibula are joined distally. Manus with 4 or 5 digits and strong curved claws; pes plantigrade with 5 digits. Tongue long and extensible. Submaxillary glands large. Stomach and uterus simple. Caeca paired or absent. Placenta discoidal. Penis large without glans; the testes are abdominal. Brain smooth, with large olfactory lobes. With one pair of pectoral mammae and an additional inguinal pair in *Tatusia*; they produce one or two young at a birth except *Tatusia*. They are all burrowing nocturnal animals, of small or moderate size, and omnivorous in their diet, eating roots, insects, worms, lizards and carrion. They are somewhat pig-like, harmless animals, usually with large external ears, and they can run and burrow with great rapidity. They inhabit the plains and forests of tropical and temperate S. America and one species (*Tatusia novem-cincta*) ranges into Texas. *Chlamydomorphus* Harlan, the pichyciego. Small animals with long silky hair differing from other dasypods in their dermal armour, and with small external ears. The body is covered with four-sided horny

\* L. J. Fitzinger, Die natürliche Familie der Gürtelthiere, *Sitzb. Akad. Wiss. Wien*, 64, 1871. Lahille, Contrib. Etud. Edentés à bandes mobile de la Rép. Argentine, *Ann. Mus. La Plata, Zool.*, 2, p. 1-30.

plates, not divided into shields and moveable bands. The bony scutes in front are very thin, but behind they form a strong shield attached to the pelvis. Vertebrae, C7, D11, L3, S10, C15. Limbs short, manus with 5 digits; with bifid caecum; 2 species. *C. truncatus* Harlan, about 5 inches long, in W. Argentina near Mendoza. *Dasypus* L., dentition  $\frac{9}{15}$  or  $\frac{8}{9}$ , of which one tooth on each side is in the premaxilla; auditory bulla complete; vertebrae C7, D11-12, L3, S8, C17-19; carapace with 6 or 7 moveable bands; tail short; manus with 5 digits; 7 species, of which 3 are found in the Pleistocene; *D. sexcinctus* L., the 6-banded armadillo *Xenurus* Wagl. (*Lysiurus* Am.), dentition  $\frac{9}{9}$  or  $\frac{8}{8}$ ; vertebrae, C7, D12-13, L3, S10, C18; carapace with 12-13 moveable bands; manus with 5 digits, of which 1 and 2 are slender and 3 has very large claw; 5 species. *X. unicinctus* L., the tatouay or cabassou. *Priodontes* Cuv. (*Priodon*), dentition variable, differing on the two sides,  $\frac{20-25}{20-25}$ ; vertebrae, C7, D12, L3, S10, C23; tail long; carapace with 12-13 moveable bands, manus with 5 digits, claw of third very large; 1 species. *P. giganteus* Geoff. (*gigas*) (Fig. 285) the largest species of the family, body 3 feet long, eats termites and insects

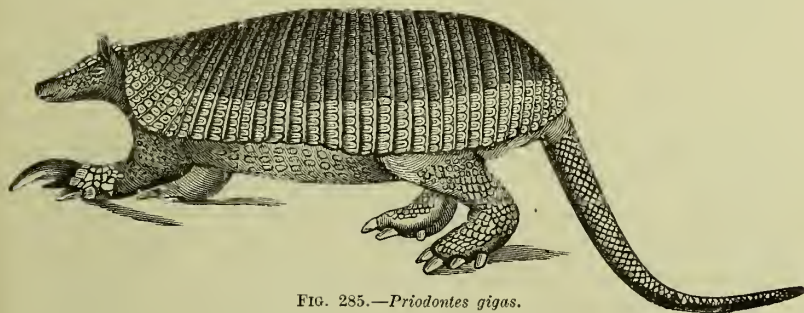


FIG. 285.—*Priodontes gigas*.

and is said to uproot newly-made graves. *Tolypeutes* Ill., dentition  $\frac{9 \text{ or } 8}{9}$ ; vertebrae C7, D11, L3, S12, C13; carapace with 3 moveable bands; tail short; manus as in preceding; can roll up into a ball; they run quickly on the tips of their toes; 3 species. *T. tricinctus* L., apar. *Tatusia* Cuv. (*Praopus*) dentition  $\frac{8 \text{ or } 8}{7 \text{ or } 7}$ , except the last with 2-rooted predecessors, which are not changed till the full size has been nearly reached; vertebrae C7, D9-11, L5, S8, C20-27; carapace with 7-9 moveable bands; manus with 4 visible toes, the 5th being small and concealed; with 2 inguinal mammae in addition to the pectoral pair, produce 4 to 10 young at a birth, about 12 species; *T. novemcincta* L., peba. *Vetelia* Am., Eocene, Patagonia; *Propaopus* Am., Pliocene, Argentina, are extinct genera allied here. *Scelopoleura* A. M. Edw. Brazil, plates on the back deficient. Extinct genera are *Chlamydotherrum* Lund., Oligocene to Pleistocene, as large as a rhinoceros; *Eutatus* P. Gervais, Pliocene; *Dasypotherium*, etc.

Fam. 7. **Glyptodontidae.** Extinct, sometimes gigantic, armadillo-like animals with a rigid carapace formed of a great number of bony scutes joined together and not divided into shields and bands; dentition  $\frac{8}{8}$ , teeth with two deep flutings on each side; zygoma with descending process from the maxilla; dorsal vertebrae ankylosed and some of the cervical;



lumbars fused with sacrum; the atlas is free; the last cervical is separate from the preceding and united with the dorsal, forming a peculiar joint allowing of the retraction of the head. Tertiaries and Pleistocene of Amer. as far as Mexico and Texas. *Glyptodon* Ow., 16-17 feet, pterygoids enter into formation of bony palate, manus with 5, pes with 4 digits; metatarsals as broad as long, several species, Pliocene of S. Amer., Pliocene and Pleistocene of Mexico, Texas and Florida. *Palaeopeltis* Am., U. Cretaceous, Patagonia; *Propalaeoplophorus* Am., about 2 feet, with premolars and molars and probably an incisor, dorsal vertebrae not fused; Eocene, Patagonia; *Palaeoplophorus* Am., Oligocene of Patagonia; *Plophorus*, Miocene, Patagonia; *Hoplophorus* Lund., medium size, Pleistocene, Argentina and Brazil; *Panoctus* Burm., very large forms, manus and pes 5-toed, Pliocene and Miocene, Argentina; *Doedicurus* Burm., manus with 3, pes with 4 digits, about 12 feet, Pliocene and Pleistocene. *Peltephilus* Am., U. Cretaceous and Eocene of Patagonia; intermediate between *Glyptodontidae* and armadillos; the glenoid part of the squamosal separated by suture from the rest (? quadrate); plates of carapace moveable; pterygoids enter hard palate; teeth in the anterior part of the jaws.

### Nomarthra (Effodientia).

The vertebrae are without accessory articulations; the ischia are not united to the sacrum. The testes lie in the inguinal canal, the penis is external; the uterus is two-horned, the vagina undivided, and the placenta diffuse or broadly zonary. They are confined to the Oriental and Ethiopian regions with fossil remains in Europe. It is extremely doubtful whether the two Old-World families which constitute this group are specially allied either to each other or to the New-World forms.

Fam. 1. **Manidae**.\* Pangolins. Edentulous, covered with large overlapping epidermal scales which can be erected, and with hairs between the scales. The tongue is long and extensile and there are large submaxillary glands. The limbs are short and carry 5 digits. They walk on the dorsal surfaces of the long claws of their fore-feet and on the soles of the pes. Skull smooth, without distinction between orbit and temporal fossa; zygoma usually incomplete; pterygoids elongated but not contributing to palate, tympanic bones bullate and united to surrounding bones, mandible without coronoid process, with flat condyle. Without clavicle; xiphoid process of sternum produced into long processes reaching as far back as the pelvis. Femur without third trochanter. Stomach with thick lining and muscular walls, and a large gland. Caecum absent. Testes inguinal, penis well developed, placenta diffuse. Terrestrial and burrowing animals one to five feet in length, can roll themselves into a ball, and some of them can climb. They feed mainly on termites.

\* Jentink, Revision of the Manidae in the Leyden Museum, *Notes Leyden Museum*, 4, 1882, p. 193. Matschie, Die natürl. Verwandtschaft etc. der Manisarten, *S.-B. Ges. Naturf. Freund. Berlin*, 1894, p. 1.



*Manis* L., with 7 species, in Burmah, Malacca, Java, Borneo, China, Formosa, Ceylon, India, Africa. Two extinct genera from the Eocene of France, *Necromanis*, *Leptomanis* Filhol.

Fam. 2. **Orycteropodidae (Tubulidentata).** Hairy body with thoracic and inguinal mammae, and long ears. Dentition diphyodont, the milk teeth not cutting the gums, <sup>8-10</sup>, not all in place at same time, the 3 posterior are without predecessors; the teeth contain parallel tubular prolongations of the central pulp-cavity. Skull with complete zygoma and well developed premaxillae, annular tympanic not ankylosed, large lacrymal; mandible slender with coronoid. Vertebrae C7, D13, L8, S6, C27. Clavicles present. Manus without pollex, pes pentadactyle; femur with a third trochanter. Tongue vermiform, submaxillary gland much developed. Stomach in two portions, a cardiac with thick lining and a muscular pyloric with thin lining. A caecum is present. Testes inguinal, descending temporarily into a scrotum; penis small. Uterus double, placenta broadly zonary. Burrowing animals, living near ant-hills; Africa. *Orycteropus* Gm., aardvark, or Cape anteaters, two species, *O. capensis* Gm., the aardvark of S. Africa; *O. aethiopicus* Sundev. N. E. Afr., extending into Egypt; an extinct species *gaudryi*, from Miocene of Samos and Persia. The extinct *Palaeorycteropus* Filhol, from the Eocene of France.

#### Order 4. SIRENIA.\* (Sea-cows.)

*Short-necked, thick-skinned, aquatic herbivorous animals, naked or with very sparse hairy covering, with separate anteriorly directed external nares, two pectoral mammae, fin-like anterior limbs and horizontally flattened caudal fin. The posterior limbs are absent.*

The Sirenia are aquatic animals, living in the sea near the coast, in estuaries and in rivers. They are herbivorous and feed on seaweed or freshwater grasses. Their bones are heavy in consequence of which they are able the more easily to lie on the bottom when they are feeding. They have small eyes, with a third eyelid, the nostrils are separate from one another and placed on the front of the head, and the ears are without pinnae. The fore-limb is paddle-like and very moveable at all its joints. The digits—five in number—are enclosed in a

\* J. F. Brandt, *Sirenae Sirenologicae*, St. Petersburg, 1846, 61 and 68. Owen, *Proc. Zool. Soc.*, 1838, p. 29. W. Turner, Placenta of Dugong; *Trans. Roy. Soc. Edinburgh*, 35, 1889, p. 641. J. Murie, On the form and structure of the manatee, *Trans. Zool. Soc.*, 8, 1872, p. 127, and 11, 1880, p. 19. A. Crane, Notes on the habits of manatees in captivity in the Brighton Aquarium, *Proc. Zool. Soc.*, 1881, p. 456. Hartlaub, Beiträge z. Kenntnis der Manatus-arten, *Zool. Jahrb.*, 1886, p. 1. Kükenenthal, Vergl. anat. u. entwick. Unters. an Sirenen, *Denkschr. Med. Nat. Ges. Jena*, 7, 1897, p. 1, and Ent. der Sirenen, *Verh. D.Z. Ges.*, 7, 1897, p. 140. R. Lydekker, Catalogue of fossil mammalia in the British Museum. H. Woodward, On the fossil and living Sirenia, *Geol. Mag.*, 2, 1885, p. 12.

common cutaneous covering, and may or may not have traces of nails. They possess the usual number of phalanges found in mammals. There are no hind limbs. The tail is horizontally expanded into a caudal fin, and there is no dorsal fin. The mammae are pectoral in position close behind the anterior limbs. The skin is thick, naked or with fine hairs scattered over it, and in the deeper layers there is a considerable quantity of blubber for which and for the skin these animals are much sought after. The neck is extremely short, and is hardly marked externally.

As already hinted, the skeleton is remarkable for its density. In the skull the anterior narial apertures are placed far back and look upwards, and the nasal bones are usually absent in living forms, though present in some extinct species, but there the resemblance to the skull of the Cetacea ends. The parietals meet in the roof; the tympanic is annular and ankylosed with the periotic, and readily comes away with the latter; the cranial cavity is small and elongated; the zygoma is very stout; the orbit is small and nearly enclosed in bone; the maxillae and premaxillae are prolonged in front of the nares as a narrow snout, which carries on its under surface a horned plate working against a similar horny plate on the mandibular symphysis; there is a large coronoid process. The dentition is variable. In *Rhytina* there are no teeth; in *Halicore* the molars ( $\frac{5 \text{ or } 6}{5 \text{ or } 6}$ ) are rootless and without enamel, and there are two tusk-like incisors in the male; in *Manatus*, there are no visible incisors and the molars are more numerous ( $\frac{11}{11}$ ) and provided with enamel and roots. The molars are never all visible at the same time, the posterior coming up as the anterior are worn away. There are milk predecessors in *Halitherium*, and in living forms there appear to be milk teeth in the foetus (see Kükenthal, *op. cit.*). The centra of the vertebrae are without epiphyses (in living forms); the cervical vertebrae (six only in *Manatus*) are compressed antero-posteriorly, but except the second and third in *Manatus* are not united. All the vertebrae have articulating processes, though these are imperfect in the caudal region, thus conferring considerable flexibility on the tail. None of them are united to form a sacrum. The ribs are mostly two-headed and the sternum is much reduced. Clavicles are absent. The scapula is normal and not like that of Cetacea.

There is a pair of bones representing the pelvis and connected with the transverse processes of the last precaudal vertebra, but in no living species is there a trace of a femur. The lips are tumid and provided with stiff bristles. Salivary glands are well developed. The stomach is divided into two portions, of which the cardiac is provided with a gland and the pyloric usually with two caeca. The large intestine has a caecum. The apex of the ventricle is cleft, and there are two superior venae cavae. Extensive retia mirabilia are formed. The diaphragm is extended very obliquely far back into the abdomen, so that the pleural cavities are prolonged dorsally to the viscera, but the heart lies in the sternal region. The brain is small and but little convoluted. The testes are abdominal; the uterus bicornuate and the placenta zonary (in *Halicore*).

As will be gathered from this account, the Sirenia present no important resemblance to whales. They differ in almost all the cranial features and in the dentition; in the structure of the well-jointed anterior limb; in the absence of a prolongation of the epiglottis and arytenoid cartilages into the nasal passage; in the small size and slight convolution of the brain. The whale-like features are the reduction of the nasal bones, the short neck, the form of the tail, and the absence of posterior limbs. By some they have been supposed to be allied to the Ungulata, but save in the form of the molar teeth in *Manatus*, it is difficult to point to any resemblance. The affinities to the Proboscidea are explained on p. 571.

There are two living genera, but a third genus *Rhytina* only became extinct in the eighteenth century, and we have descriptions of its appearance and soft part. They are purely aquatic and never come on to the land. They inhabit shallow seas near the coast, estuaries, and rivers which they ascend sometimes almost to their source. They feed on sea-weeds and aquatic plants. They are gregarious, slow, inoffensive, gentle creatures, qualities which render them an easy prey to the hunter, and which brought about the entire destruction of the *Rhytina*. They are sought after for their flesh as food, for the oil derived from the fat beneath their skins and for their hides. They use their limbs as hands for conveying food to the mouth, and they are said to carry their young pressed

to the breast with their flipper. This fact (if true) together with the pectoral position of the mammae, and the habit they have of raising their head out of the water, may have given origin to the legend of mermaids.

Numerous remains of Sirenians are known in the Miocene and Pliocene of Europe and N. America.

*Manatus* Storr (*Trichechus*), manatee; to 8 feet; dentition \*  $i \frac{2}{3}$ ,  $m \frac{1}{11}$ , the incisors lie beneath the horny plates on the jaws and disappear before maturity, the molars are rooted (3 roots in the upper and 2 in the lower jaw), and have enamelled crowns with two tuberculated transverse ridges, they come into use gradually, there never being more than  $\frac{2}{3}$  functional at the same time; rostrum not bent downwards; upper lip bifid and used in feeding; vertebrae C6, D17, L2, C23 to 35; tail entire and rounded; manus with vestiges of two or three nails; caecum bifid. Mainly fluvatile, but also marine; shores of and the great rivers emptying into the Atlantic Ocean within the tropics; 3 species on the American side and 1 on the African. Allied extinct genera are *Manatherium* Hartlaub, Oligocene, Europe; *Ribodon* Am., Oligocene, Patagonia. *Halicore* Illig., dugong, to 8 feet,  $i \frac{2}{4}$   $m \frac{5 \text{ or } 6}{5 \text{ or } 6}$ ; the anterior upper incisor is tusk-like and projects in the male, but is not cut in the female, the posterior upper incisor is found only in the young; the lower incisors lie beneath the horny plate and are soon absorbed, the molars are without roots and enamel and have tuberculated crowns which wear down to flat surfaces. The rostrum of the skull is bent downwards. Vertebrae C7, D18-19, L and C30. Tail notched and whale-like. Manus without nails. Caecum single. Mainly marine, shores of the Red Sea, Indian Ocean, Australia, 3 species have been distinguished. *Rhytina* Ill., Steller's sea-cow, 20-25 feet, recently extinct, about 1768, Behring and Copper Islands in Behring Straits, discovered by Behring and Steller, who were wrecked upon Behring Island in 1741. Its flesh and fat were exceedingly delicious, and it was used as food by them and later mariners. Owing to its gentleness and fearlessness of man, it was easily slaughtered and soon became extinct. It was edentulous, had the horny pads on the jaws, was without nails but had bristles on its manus. Its vertebrae had epiphyses. *Hali-therium* Kaup, Oligocene of Europe, Eocene of America; with large tusk-like incisors in the upper jaw,  $\frac{2}{3}$  or  $\frac{6}{6}$  molars, well enamelled and tuberculated ridged crowns; there appear to have been milk teeth; sometimes with normal but small nasal bones; pelvis better developed with short femur. A number of other genera are known from the Miocene and Pliocene of Europe and America. *Prorastomus* Ow., Eocene of Jamaica and Europe is the oldest form known, with dentition  $i \frac{3}{3}$   $c \frac{1}{1}$   $p$  and  $m \frac{2}{2}$ , incisors not tusk-like.

\* According to Kükenthal (*loc. cit.*) there are calcified rudiments of canines in the lower jaw of the embryo, and of milk predecessors of some of the teeth.



## Order 5. CETACEA.\*

*Aquatic, fish-like, naked forms without hind limbs. The head passes continuously into the body and the nasal apertures are on the top of the head.*

The Cetacea are entirely aquatic animals. Though fish-like in appearance, they are mammalian in structure, but they stand far apart from other mammals, and it is impossible to guess at their origin. Some species attain a colossal size, and are among the largest, if not the largest, of all known animals, whether living or extinct. The cervical region of the vertebral column is extremely short, and there is apparently no neck, the head passing directly into the trunk. There is a horizontally-expanded caudal fin (the lateral expansions of which are called *flukes*), and often a fatty dorsal fin. Hairs are almost entirely absent, being represented only by a few bristles on the upper lip, which are present during the whole of life or only during the foetal period, and are without sebaceous glands. On the other hand there is developed beneath the thick skin in the subdermal cellular tissue a considerable layer of fat (blubber), which to a certain extent takes the place of fur and serves both to prevent the loss of heat and to diminish the specific gravity. It does not, however, necessarily follow that the absence of hair is caused by the presence of blubber, for in the seals both hair and blubber are present. The absence of hair is a property of the whale, and cannot be accounted for. The same remark applies to the scanty hairy covering found in some other mammals. The head is large, and the opening of the external ear is very minute and without a pianna. The eyes are

\* Hunter, Observations on the structure and oeconomy of whales. *Phil. Trans.*, 1787. F. Cuvier, *Histoire naturelle des Cétacés*, Paris, 1836. D. F. Eschricht. *Unters. über die nordischen Walthiere*, Leipzig, 1849. D. F. Eschricht og J. Reinhardt, *Om Nordhvalen*, Copenhagen, 1861. van Beneden and Gervais, *Osteographie des Cétacés viv. et foss.*, 1868-1880, 1 vol. and atlas 64 plates. van Beneden, *Histoire Nat. des Cétacés des mers d'Europe*, 1 vol. 8vo, 1889. C. M. Scammon, *Marine Animals of the N.W. coast of N. America*, 1874. J. F. Brandt, *Unters. üb. die foss. u. subfoss. Cetaceen Europa's*, *Mem. Acad. Petersbourg*, (7), 20, and 21, 1873-4. W. H. Flower, On the characters and divisions of the families of the *Delphinidae*. *Proc. Zool. Soc.*, 1883, p. 466. F. W. True, Review of the Family *Delphinidae*, *Bull. U. S. Nat. Mus.*, 1889. R. Lydekker, Cetacea of the Suffolk Crag, *Quart. Journ. Geol. Soc.*, 42, 1887, p. 7, and *Catalogue of the fossil mammalia in the British Museum*, 1887. F. E. Beddard, *A Book of Whales*, London, 1900.





The hard and dense petrous bone is loosely united with the squamosal, and may or may not be ankylosed to the tympanic; it readily falls out in the dry skull. The tympanic bones are thick and scroll-like. These bones are of great importance to the palaeontologist, for they are found wherever fossil remains of Cetacea occur, and were dredged up from the ocean bed in considerable numbers by the *Challenger*. The frontal bones are prolonged into a plate on each side which covers the orbit. The squamosal sends forward a strong process which meets this supraorbital part of the frontal. The jugal is usually a slender bone, underlying the orbit and extending from the maxilla to the strong zygomatic process of the squamosal. The maxillae are prolonged forwards almost to the front of the snout, and with them, on their median sides, extend the long premaxillae from the nasal aperture to the end of the snout, where they contribute for a small area to the margin of the mouth. The premaxillae do not bear teeth except in *Squalodon* and *Zeuglodon*. The snout is composed of these two bones, and of the vomer and mesethmoid cartilage. The nasals are short and united to the frontal bones immediately behind the nares; they are often asymmetrical. Distinct lacrymals are present in some whalebone whales, and in the Physeteridae. The nasal passages are almost vertical and the turbinals are vestigial. The pterygoids frequently meet and take part in forming the hard palate. The mandible has a very small coronoid process. The hyoid is a broad plate of bone, and has two pairs of cornua.

Teeth are sometimes absent. They have conical or compressed crowns, are homodont (except *Zeuglodon* and *Squalodon*) and monophyodont, and are often very numerous.

In the whalebone whales, which have no teeth in the adult, there is in the foetus a set of minute calcified \* teeth, some of which are provided with two or even three cusps. Kükenthal maintains that these are rudiments of the milk dentition, and that he has detected traces of a successional series. Kükenthal also maintains that he has detected traces of successional teeth in some of the toothed whales, and that the persistent teeth in these belong in reality to the milk dentition.

The vertebral column is distinguished by the thin disc-like character of the cervical vertebrae which are usually more or less fused together (especially in *Balaena*); by the relatively

\* Julin, *Arch. de. Biologie*, 1, 1880.

large number of lumbar and caudal vertebrae, the latter having chevron bones; by the absence of sacral vertebrae and by the thick fibrous intervertebral discs and the absence of articulating processes on the posterior dorsal and hinder vertebrae. The epiphyses of the vertebrae and of other bones remain distinct for some time. The number of vertebrae is C7, D9-16, L3-24, C18-30. The sternum tends to be short and but few ribs join it. The ribs are distinguished by their loose articulation both with sternum and vertebral column. There are no clavicles. The scapula is remarkable for the position of the spine close to the anterior border. The humerus is short and freely moveable upon the scapula, but the other joints of the fore-limb are imperfect. The radius and ulna are flattened and short. The carpal bones are more or less normal and embedded in fibrous tissue, but they vary considerably. In the whalebone whales many of the elements of the manus (including the phalanges) remain cartilaginous. There are generally five digits, but in most of the whalebone whales there are only four.\* There are more than three phalanges in some of the digits: this always happens in digits Nos. 2 and 3, in which the number may mount to fourteen or more. The phalanges have epiphyses at both ends.

The pelvis is represented by a pair of bones placed longitudinally at some distance from the vertebral column, and probably representing the ischia. The crura penis are attached to them, and in the whalebone whales there may also be a trace of the femur in the form of a short bony rod attached to their outer sides, to which may be added the trace of a tibia.

The brain is very large and its surface richly convoluted. It is the largest and most convoluted brain found beneath the Primates. The lateral ventricle shows a trace of a posterior cornu. The olfactory lobes and nerves are absent or small.

The soft palate is long and muscular. The glottis is funnel-shaped, owing to the prolongation of the epiglottis and arytenoid cartilages, which project into the narial passage. When this spout-like structure is embraced by the soft palate there is a

\* In such cases it has been said that it is digit No. 3 which has dropped out; vide Kükenthal (*Denkschr. Med. Nat. Ges. Jena*, 3, 1889, p. 1, and 3, 1893, p. 221) who maintains that in a foetal *Balaenoptera* there is a trace of a digit, which does not reach the carpus, between digits Nos. 2 and 3, and that in the pentadactyle *Balaena* the first digit is a prepollex.

continuous passage between the narial passage and the larynx. The trachea is very short, and gives off a third bronchus to the right lung just before it divides. The lungs are very spacious and not lobed; they extend, like the swimming bladder of fishes, far backward, and play an essential part in the maintenance of the horizontal position in water. The diaphragm also has a corresponding horizontal extension, as it has in the Sirenia. The stomach is complicated and divided into three or more chambers. In *Phocaena* (Fig. 287) the oesophagus opens into a large elongated blind sac lined by a thick epithelium; near the oesophageal end of this is the opening into the second chamber, the lining of which is soft and vascular and projects in longitudinal folds into the cavity. The third chamber is tubular, and possesses a small globular dilatation at its commencement; it opens into the duodenum, the commencement

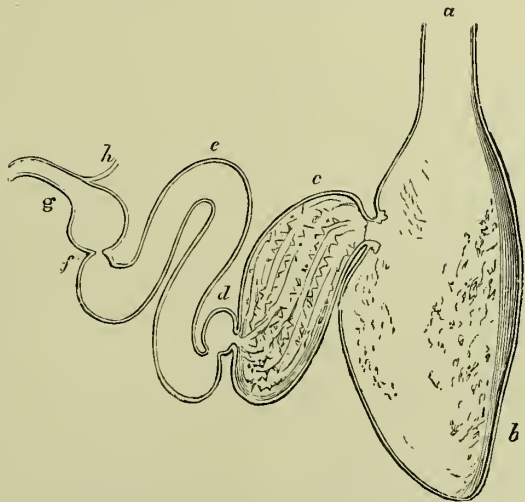


FIG. 287.—Diagrammatic section of the stomach of a porpoise (from Flower and Lydekker). *a* oesophagus *b* cardiac chamber, *c* middle chamber, *d* and *e* two divisions of the third or pyloric chamber, *f* pylorus, *g* duodenum, *h* bile-duct.

of which is dilated and receives the conjoined bile and pancreatic ducts. In Ziphioids\* the first chamber is absent, or combined with the second, and the pyloric chamber is divided up into seven or eight chambers by successive constrictions.

There are saccular dilatations on the aorta and pulmonary arteries, and retia mirabilia on the arteries, particularly those under the pleura and between the ribs, and on the veins. The use of these is not understood, but they are supposed to be connected in some way with the power these animals have of

\* Jungklaus, *Jen. Zeitschr.*, 32, 1898, p. 1.

remaining for a long time under water. The aorta in the sperm-whale is a foot in diameter, and the heart sends out at each stroke probably ten or fifteen gallons of blood. The kidneys are lobulated. The testes are abdominal and in contact with the ventral body wall, at about the level of the anterior end of the bladder, and there are no vesiculæ seminales. The penis is large and there is no os penis. The uterus is bicoanuate and the placenta diffuse. The females bear a single (the smaller species rarely two) young at a birth. There are two mammae, inguinal in position; the teats lying in depressions on each side of the vulva.

The Cetacea usually live together in herds (schools). The smaller species frequent the coasts and some of them ascend rivers; others are mainly fluviatile. The larger species prefer the open sea. They swim with great strength and speed, usually keeping near the surface, to which they have frequently to ascend for respiration. They can stay under the surface for a long time. Some of the larger whales can remain submerged for more than an hour, certainly for two hours and possibly for more. The spouting or blowing of whales is not a spout of water ejected from the nostrils, but is due to the condensation in the cold atmosphere of the aqueous vapour of the column of warm and compressed expired air, which issues with great force when the animal reaches the surface.

The Cetacea are carnivorous predaceous animals. Most of them feed on small marine organisms and on fish and cephalopods. The gigantic whalebone whales, which are without teeth, but possess whalebone on the palate, feed on small floating marine animals, nudibranchiate molluscs and jelly fish, etc. They are animals of great intelligence and generally of a mild disposition. The cows display great affection for their calves, and it is this feature which is often taken advantage of by whalers in their pursuit of them, for the mother will rarely desert her weaker offspring. If the latter is wounded or killed, the mother will turn upon her pursuers with fury, and deal destruction to the boats and death to the men. But it is rarely that whales will attack men if unprovoked. The sperm-whale is apparently an exception to this, for there appear to be several authentic instances of a cachalot having attacked a ship and done it severe damage, even sinking it. But in these cases it is pro-



bable that the monster was provoked by the ship having accidentally come into contact with it. Whaling is the finest sport known to man. It requires great skill and knowledge, and all the strongest qualities of human nature. Indeed, other sports may be called child's play as compared with it. It is generally carried on in the wildest and most terrible places of the earth, and the quarry is by far the largest and most powerful of animals now living, and the most profitable to capture. A fine whale of the "right" kind will yield upwards of three hundred barrels of oil and considerably over a ton of whalebone.\* So inveterately have some of these animals been pursued that they appear to be on the verge of extinction. The Atlantic right-whale has entirely forsaken its former grounds, the black whales of the southern temperate ocean have been almost entirely exterminated; and Captain Scammon says of the Californian grey whale that "ere long it may be questioned whether this mammal will not be numbered among the extinct species of the Pacific." As an illustration of the same fact, it may be mentioned that between the years 1788 and 1879, 4,195 Greenland whales were brought into Peterhead, while in 1891 only 17 whales were captured, and a few years ago the catch by Dundee whalers was only six.

The period of gestation is not certainly known, but in the case of the larger species it is stated by Scammon to be from nine to twelve months. Coition is probably effected with the animals lying breast to breast, either horizontally on the surface of the sea or in a vertical position. Their amatory antics, which have sometimes been observed, are highly entertaining. "Their caresses are of the most amusing and novel character. When lying by the side of each other, the megapteras frequently administer alternate blows with their long fins, which love-pats may, on a still day, be heard at a distance of miles. They also rub each other with these same huge and flexible arms, rolling occasionally from side to side and indulging in other gambols, which can easier be imagined than described."† They are found in all seas, and their fossils occur in the Tertiary

\* The price of whalebone varies considerably. At the beginning of the fifteenth century it was about £150 a ton; in 1891 whalebone of good quality brought £2,800 a ton.

† Scammon, *op. cit.*, p. 45. The same authority has estimated their duration of life at from thirty to a hundred years.

deposits. The earliest known form is Zeuglodon from the Eocene.

### Sub-order 1. MYSTACOCETI (BALAENOIDEA.)

The whalebone whales, with large head, without teeth in the jaws, with whalebone (baleen) hanging from the palate. The oesophagus is narrow, there are two spiracles (external narial openings), and the nasal passages are without saccular dilations. Manus tetradactyle except in *Balaena*.

Fam. 1. **Balaenidae.** Teeth are absent in the adult state, but numerous minute calcified teeth are present in both jaws in the foetus. The whalebone or baleen consists of a number of horny triangular plates which are arranged in a row on each side of the palate and hang down into the mouth. The outer edge of the plate is smooth, its base is attached to a transverse ridge of the palate, and its inner edge is frayed out into

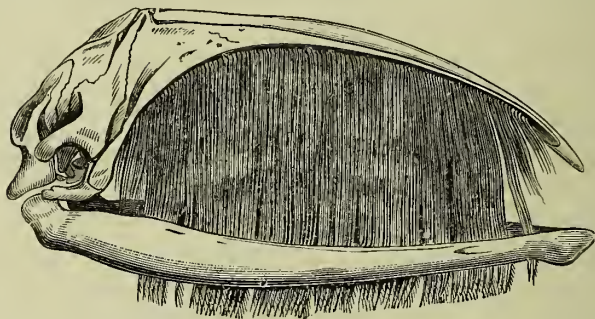


FIG. 288.—Skull of *Balaena mysticetus*, with the whalebone (Règne animal).

numerous filamentous processes. A vascular lamella extends from the palate into the base of each plate. From this there projects a number of vascular papillae which extend into the free bristle-like fibres. The epithelium round these papillae is cornified, and in the proximal region gives rise to a connecting substance ("enamel") which forms the smooth outer substance of the plate, and with the contained fibres constitutes the plate. Peripherally this connecting substance breaks down and the fibres become free. The "gum" (intermediate substance) is a mass of thickened epithelium between the bases of the plates. In feeding, the animal opens its mouth so that the baleen plates hang vertically downwards. In *Balaena*, in which the plates are very long, their lower ends rest on the base of the mouth within the lower lips which prevent their bending outwards when the mouth is closed. The animal then closes its mouth and the water is driven out through the strainer formed by the plates and their fibres. It then swallows by the help of its tongue the organisms which are retained by the strainer. The ends of the plates and their fibres fold backwards when the mouth is closed.

The skull is symmetrical, and the nasal bones are larger than in other

Cetacea. The maxilla is produced in front of, but not over, the orbital process of the frontal. The lacrymal bone is distinct and the tympanic is ankylosed with the periotic. The rami of the mandible are convex outwards, and the space between them is greater than the width of the rostrum; they are connected by ligament at the symphysis. The ribs articulate with the ends of the transverse processes, the capitular part being imperfect and not reaching the centrum. The sternum is short and articulates with only one pair of ribs. Olfactory nerves and a small olfactory organ are present.

The family includes the right-whales and the rorquals or fin-whales.

*Balaena* L., right-whales, skin of throat smooth, no dorsal fin. *B. mysticetus* L., Greenland or Arctic right-whale; Arctic Ocean; from 45 to 50 feet; 380 baleen plates or more, the longest 10 to 12 feet. *B. australis* Desmoul., the southern right-whale, temperate seas of both hemispheres; smaller head and shorter baleen; has been so much pursued that it is now very scarce. Several extinct species in the Pliocene of Europe and America. *Neobalaena* Gray, skin of throat smooth, a small dorsal fin, to 20 feet, baleen very long and white. 1 species, *N. marginata* Gray, New Zealand and Australian seas. *Rhachianectes* Cope, 1 species, *R. glaucus*, the grey whale of the N. Pacific. *Megaptera* Gray, with dorsal fin, skin of throat plicated and long pectoral fins. *M. boops* L., hump-back whale, 45 to 50 feet, Atlantic and Pacific; several Pliocene species. *Balaenoptera* \* Lacép, rorquals, head small, skin of throat plicated, dorsal fin present, body long and slender, cervical vertebrae free; in all seas; whalebone inferior and blubber scanty. *B. sibbaldi* Gray, blue whale, the largest known, to 85 feet; Atlantic, Arctic Oceans. *B. musculus* L., common rorqual, 65 to 70 feet, Atlantic and Arctic; and many other species; many extinct species from the Pliocene. Several extinct genera from the Miocene onwards, e.g. *Cetotherium* Brandt, *Herpetocetus* v. Ben., *Plesiocetus* v. Ben., etc.

## Sub-order 2. ODONTOCETI (DELPHINOIDEA).

In the toothed-whales, conical calcified teeth, often in great number, are always present after birth. The external nares are united to a single semilunar opening, and saccular dilations lying between the skin and the skull are developed in the passage which connects the opening with the narial passages. The upper surface of the skull is more or less asymmetrical, and the superior maxillary bone is posteriorly expanded and spread out over the supraorbital process of the frontal. The nasal bones are reduced to mere nodules, and take no part in roofing over the narial passage. Lacrymal absent except in the Physeteridae. Tympanic not ankylosed to the periotic. Rami of the mandible straight and meeting in a symphysis. Anterior ribs two-headed. Sternum usually composed of several pieces and connected with several ribs. Manus always pentadactyle. Caecum absent.

\* v. Beneden, Les Balénoptères, etc., *Mem. Cour. Ac. Belg.*, 41, 1888.

Fam. 2. **Physeteridae.** With functional teeth in the lower jaw only ; asymmetry of skull strongly marked. The maxillary and frontal bones are spread out and produced so as to form on the upper and anterior surface of the skull a basin, which is loaded with fat. The pterygoids have palatal plates, and the mandibular symphysis is elongated. The lacrymals are large and usually distinct. Most of the cervical vertebrae are ankylosed. The posterior ribs lose their tubercular attachment, but retain the capitular, a process arising on the centrum to meet the latter. Fossil forms are known from the Eocene onwards in Europe, America and Australia.

Sub-fam. 1. **Physeterinae.** Sperm-whales. With an enormous head, swollen to the extremity by the accumulation of fat (spermaceti) ; upper jaw without functional teeth, though functionless teeth embedded in the gums are present ; mandibular teeth set in a groove, not in sockets. Lacrymal bone not distinct. Cranial basin filled with spermaceti. *Physeter* L., cachalot or sperm whale ; one species, *P. macrocephalus* L., from 55 to 60 feet, the female being smaller ; zygomatic process of the jugal thick ; in all tropical and sub-tropical seas ; food consists principally of cephalopods ; it has a large throat ; *ambergris*, a concretinary substance, is a product of and found in the alimentary canal of the cachalot, and has great commercial value ; spermaceti and sperm oil are obtained from this whale ; the spermaceti is found mixed with the fat all over the body where fat occurs, but the principal accumulation is in the cranial basin. *Kogia* (*Cogia*) Gray, with smaller head, slender jugal, teeth in upper jaw absent or only two ; length 10 feet ; rare form, Southern Ocean, Madras, and N. Pacific. Extinct genera, *Diaphorocetus* Am., U. Eocene, America, *Physodon* Gerv., *Hoplocetus* Gerv., and other genera from the Miocene onwards.

Sub-fam. 2. **Ziphiinae.** With only one or two pairs of fully formed teeth in the mandible, the rest concealed in the gums ; anterior part of mesethmoid usually ossified ; lacrymal distinct ; feed on cephalopods. *Hyperoodon* Lacép., bottlenose, skull with largely developed maxillary crests in the male, with spermaceti in upper part of head, length 30 feet ; N. Atlantic ; they dive deep for food, remain under some time ; jump out of the water and return head first ; fossil in the Red Crag. *Ziphius* Cuv., *Mesoplodon* Gervais, Seas of N. and S. Hemispheres and in Red Crag. *Berardius* Duvernoy, N. Zealand seas. Extinct genera from the Miocene onwards.

Fam. 3. **Squalodontidae.** Extinct forms from the Eocene, Miocene, Pliocene and possibly Pleistocene, known by their teeth and skulls ; with teeth in the premaxillae and heterodont dentition,  $i \frac{3}{4}$ ,  $c \frac{1}{4}$ ,  $p \frac{1}{4}$ ,  $m \frac{7}{8}$  ; the premolars conical and one-rooted ; the molars compressed, serrated, especially posteriorly, and two-rooted. The skull like that of other Odontoceti with reduced nasals, and posteriorly placed nostrils. *Squalodon* Grat., Miocene and onwards ; *Prosqualodon* Lyd., Eocene, Patagonia ; *Phococetus* Gerv., Eocene, France.

Fam. 4. **Platanistidae.** Fluvatile or estuarine, in the Ganges and rivers of S. America. Rostrum much elongated and narrow, upper and lower jaws with numerous conical one-rooted teeth, premaxillae without teeth, mandibular symphysis very long, orbit very small, lacrymal distinct, cervical vertebrae all separate ; the tubercula and capitula of the ribs



blend posteriorly in the normal mammalian fashion; *Platanista* Wagl., the maxillae are much expanded posteriorly and arched upwards so as nearly to meet above the narial openings, blind eyes vestigial without lens; 8 feet, feeds on small fish and crustacea, Ganges, Brahmaputra, and Indus. *Inia* D'Orb., 7 feet, Upper Amazon. *Pontoporia* Gray, 5 feet, mouth of the Rio de la Plata. *Extinct genera*, *Argyrocetus* Lyd., Eocene, Patagonia; *Pontistes* Burm., and *Pontiraga* Am., U. Eocene, Argentina; and other genera from the Miocene and Pliocene of Europe and America.

Fam. 5. **Delphinidae.** The teeth are numerous in both jaws except in the narwhal; the rostrum is of moderate length and the symphysis of the mandibles does not extend for more than one-third the length of the lower jaw; the maxillae and frontals are not markedly produced upwards at their edges; lacrymals not distinct; pterygoids frequently meet. Anterior ribs two-headed, posteriorly they lose their capitula and remain articulated to the transverse processes only. Sternal ribs ossified. A large group of living forms, found in all seas, many will ascend rivers in search of food; about 19 genera and 50 to 100 species; extinct species of existing genera from the Miocene onwards.

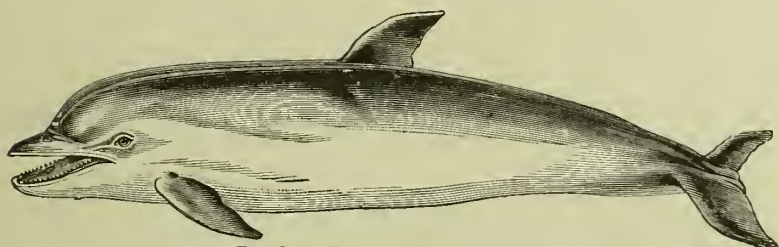


FIG. 289.—*Delphinus delphis* (Règne animal).

A. Head rounded, without distinct beak; rostrum about as long as cranium.

*Monodon* L., the narwhal, the entire dentition (save for some irregular vestiges) is suppressed except two large teeth in the front of the maxilla; one (the left) of these, and sometimes both, project in the male as long (7 to 8 feet) spirally grooved tusks; in the female they both remain in the alveolus; a second pair of small teeth has been detected behind the tusks in the foetus; pterygoids wide apart; cervical vertebrae mostly distinct; with distinct neck and no dorsal fin; 1 species. *M. monoceros* L., the use of the tusk is unknown, Arctic Ocean; there is a Pliocene species. *Delphinapterus* Lacép., like the last, but without tusks, dentition  $\frac{8 \text{ to } 10}{8 \text{ to } 10}$ ; the only species, *D. leucas* Pall., the white-whale or beluga, 12 feet, Arctic seas; Miocene and Pliocene species are known. *Neomeris* Gray, Indian Ocean. *Phocaena* Cuv., porpoise, dentition  $\frac{2 \frac{5}{8}}{2 \frac{5}{8}}$ , teeth with compressed crowns; both this and the previous genus sometimes possess a patch of small horny tubercles on the back\*; three species; *Ph. communis* Cuv., feeds on fish, Atlantic and Pacific, not Mediterranean. *Cephalorhynchus* Gray, about 3 species. *Orcella* Gray, Indian Ocean and Irrawaddy, 1 species. *Orca* Gray, the killer, white and yellow on black, to

\* They are also found on the head and front of the flipper, and dermal calcifications are found in connection with them. Kükenthal, *Anat. Anz.* 5, 1890, p. 237.



30 feet; distinguished from all other cetaceans by preying upon fish, seals, and other cetaceans, with high dorsal fin, dentition about  $\frac{1}{2}$ , 2 species, all seas from Greenland to Tasmania; a Pliocene species known. *Pseudorca* Reinhardt, all seas, 1 species. *Globicephalus* Less., nearly all seas; 6 species; *G. melas* Traill, the pilot whale, ca'ing whale, 20 feet, very gregarious and easily destroyed, dentition  $\frac{8 \text{ to } 12}{8 \text{ to } 12}$ . *Grampus* Gray, Atlantic, Pacific, Mediterranean; teeth absent in lower jaw, in the mandible 3-7 on each side near the symphysis; 1 species. *Feresa* Gray. *Lagenorhynchus* Gray, teeth small,  $\frac{23 \text{ to } 33}{23 \text{ to } 33}$ , 9 species.

B. Head with beak; rostrum of skull longer than the cranium; atlas and axis united, other cervicals separate. Porpoises and dolphins.

*Delphinus* L., teeth  $\frac{40 \text{ to } 60}{40 \text{ to } 60}$ , small, close set; pterygoids meeting in the palate; digits 2 and 3 well developed, rest rudimentary; 4 species. *D. delphis* L., in all seas, common dolphin of the Mediterranean; 7 feet. *Tursiops* Gervais, 5 species. *Tursio* Wagl., 2 species. *Prodelphinus* Gervais; 9 species. *Steno* Gray; 2 species. *Sotalia* Gray, 8 species, mostly fluviatile or estuarine; *S. teuszii*, Cameroon river, fresh-water and apparently herbivorous. *S. sinensis* Flower, Chinese white dolphin; *S. tucuxi* Gray, from the Amazon.

### Sub-Order 3. ZEUGLODONTA\* (ARCHAEOCETI).

Eocene forms of doubtful affinity. The remains upon which the group is based being imperfect it is impossible to arrive at certainty as to whether they should be regarded as primitive Cetacea or as being allied to the pinnipede Carnivora. They were animals of considerable size, attaining a length of over 60 feet. They are said to have had an armour of dermal plates.† The head is elongated and depressed, the nasal bones being long and the external nares in front on the upper side of the snout. The parietals meet in the sagittal suture, and the sagittal crest is well developed. The frontal roofs over the orbit, and is not overlaid by the maxilla. The cranial cavity is small. These are all non-cetacean characters, and it is difficult to see on what grounds such a head as this can be regarded as belonging to that order. To these points of unlikeness we may add the following. The premaxillae bear teeth and take part in forming the edge of the upper jaw. The dentition is heterodont,  $p \frac{3}{3} c \frac{1}{1} p$  and  $m \frac{5}{5}$ , the posterior molars being laterally compressed with two roots and serrated edges like the molars of seals. The cervical vertebrae are separate and not compressed. The ribs are two-headed and the sternum is composed of several pieces. The lumbar vertebrae have elongated bodies. The limbs with the exception of a mutilated humerus are unknown. Although the four last-named characters are not inconsistent with cetacean affinity, they cannot be regarded as proofs of it, when due weight is allowed to the non-cetacean features of the skull. We have however followed the usual practice of assigning the single genus *Zeuglodon* Owen to the Cetacea; Eocene of N. America, Europe, Egypt, and N. Zealand.

\* D'A. W. Thompson, On the systematic position of *Zeuglodon*, *Studies from the Museum of Zoology of Dundee*, 1890. W. Dames, Ueb. *Zeuglodonten aus Aegypten etc.*, *Pal. Abh.* 3, heft 5, 1894, p. 1. R. Lydekker, *Proc. Zool. Soc.*, 1892, p. 560.

† Abel, *Mem. Mus. Belgique*, 1, 1901.

Order 6. **HYRACOIDEA.\***

*Rodent-like plantigrade creatures of small size, with tetradactyl manus and tridactyl pes, short ears and reduced tail. The grinders are rhinocerotine, and there is a centrale in the carpus.*

The affinities of this order are difficult to understand. They have been associated with the Rodentia and with the Ungulata. They are certainly not rodents, and except in the back-teeth it is difficult to see any ungulate features. We have therefore, following Huxley, given them the rank of an order.

They have close set fur, small ears, and a split snout. The digits have nails, except digit No. 2 of the pes which has a curved claw.

The dentition is  $i \frac{1}{2}$ ,  $c \frac{1}{0}$ ,  $p \frac{1}{4}$ ,  $m \frac{3}{3}$ . The upper incisors have persistent pulps, enamel on the anterior side only and are curved as in rodents; they differ from the corresponding teeth of rodents in being pointed. The lower incisors have denticulated crowns and bite behind the upper. There is a diastema and the grinders are lophodont and like those of the rhinoceros. The milk dentition is  $i \frac{3}{2}$ ,  $c \frac{1}{1}$ ,  $m \frac{4}{4}$ , the upper incisors being rooted.

The jugal extends forwards to the lacrymal and takes part in forming the glenoid cavity which is transversely placed. The postorbital process of the skull (mainly from the parietal) is considerable and nearly meets the jugal. There is an alisphenoid canal. The premaxillae are large. In the vertebral column there are from 28 to 30 dorso-lumbar vertebrae, of which twenty-one or twenty-two are dorsal. There are no clavicles, and the spine of the scapula is without an acromion. The ulna and fibula are complete, and there is a vestige of the pollex. The carpus (Fig. 290) has a centrale and the bones of the two rows do not alternate. The femur has a small third trochanter. In the pes (Fig. 290) digits 1 and 2 are entirely absent, and the ungual phalanx of digit 2 is cleft. The astragalus presents a shelf on

\* J. F. Brandt, Unters. üb. d. Gattung Hyrax, *Mem. Ac. imp. Sci. Petersbourg*, 1869, (6), 14. O. Thomas, On the species of Hyracoidea, *Proc. Zool. Soc.* 1892, p. 50. M. Woodward, On the milk dentition of Procavia, *Proc. Zool. Soc.* 1892, p. 38. George, *Ann. Sci. Nat.*, (6), 1, 1874. Ameghino, Mammifères Crétacés de l'Argentine, *Bol. Inst. Geogr. Arg.*, 18, 1897. Fischer, Bau u. Entw. des Carpus u. Tarsus vom Hyrax, *Jen. Zeitschr.*, 37, 1903, p. 691.

its inner side for the articulation of a process of the tibia. The fibula articulates with the astragalus, not with the calcaneum. The stomach is simple. There is the usual caecum at the

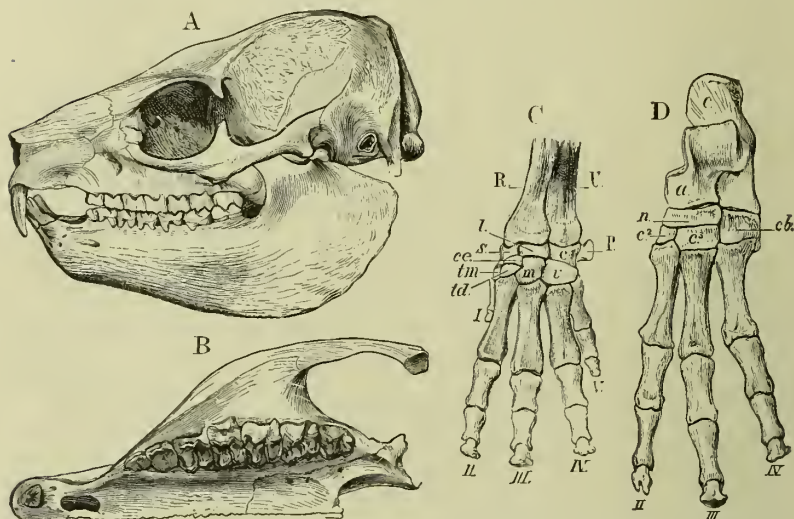


FIG. 290.—*Procavia arborea* Smith, Cape of Good Hope. A skull. B upper jaw from below. C manus, D pes (from Zittel). R radius, U ulna, s scaphoid, l lunar, c cuneiform, p pisiform, ce centrale, tm trapezium, td trapezoid, m magnum, u unciform, c calcaneum, a astragalus, n navicular, c², c³ meso- and ecto-cuneiform, cb cuboid, i-v digits numbered.

beginning of the large intestine, and a pair of smaller caeca placed lower down on the colon. There is no gall bladder. The testes remain in the abdomen and there is no scrotum. The vulva and anus are enclosed in a common fold of skin. There



FIG. 291.—*Procavia syriaca* (from Claus).

are six mammae, four of which are inguinal and two axillary. The uterus is bicornuate and the placenta zonary. Most of the species live on rocky ground, but a few (the *Dendrohyrax* division) live in trees.

There is one living genus, *Procavia* Storr (*Hyrax* Herm.), represented by about 18 species in Africa; one of these, *P. syriaca* Schreb., extends into Syria; it is the coney of the Bible. *P. capensis* Pall, rock-rabbit, daman, dassy. The earliest remains of these animals hitherto found are from the Upper Eocene of the Fayum in Egypt. These are *Megalohyrax*

Andrews,\* about the size of a tapir, with a third incisor and premolariform canine, and *Saghatherium* Andrews and Beadnell.† These forms are similar to those now existing, and present all the peculiar features of specialisation of the order. The skull of a fossil species, *Pliohyrax* (*Procavia*) *kruppii*, is known from the Miocene of Samos, and recently Ameghino has described remains from the Cretaceous and Lower Eocene of Patagonia under the names of *Archaeohyrax*, *Argyrohyrax*, *Plagiarthrus*.

### Order 7. PROBOSCIDEA. ‡

*Large pachyderms with long proboscis which is used as a prehensile organ; with large lophodont grinding teeth, and tusks in the premaxillae or mandible.*

The peculiar gait of elephants is due to the fact that the legs are not bent at the elbow and knee as is the case in most quadrupeds but as in *Dinoceras* and *Titanotherium* depend vertically from the body. They walk with the tips of their toes on the ground, but the weight is mainly carried by a great cushion on the posterior surface of the digits, so that they may be described as semiplantigrade. The toes are not separate externally but their termination is marked by nails, which are not, however, always as numerous as the digits.

The body is covered by a thick skin which in the living forms is only sparsely covered with hairs. The head is enormous, being short and deep, and the skull is swollen by air-chambers in the frontal, parietal, premaxillary, maxillary, nasal, palatal, and other bones. All these air-spaces communicate with the nasal passages. The apertures of the external nostrils are placed at the end of a long trunk, which is extremely mobile and

\* Andrews, *Geological Magazine*, 4, 10, 1903, p. 341.

† Andrews and Beadnell, *A preliminary note on some new mammals from the Upper Eocene of Egypt*, Cairo, 1902.

‡ Kaup, *Description d'ossem. de foss. Mammifères*, 1832-35, Cah. i. and iv.; *Acten der Urwelt*, 1841, 1. Lartet, *Sur la dentition des Prob. foss.* etc., *Bull. Soc. Geol. France*, 1859, 16. Falconer and Cautley, *Fauna antiqua sivalensis*, 1846. Falconer, *On the species of Mastodon and Elephant, fossil in Gt. Britain*; Pt. 1, *Mastodon*, Pt. 2, *Elephant*, *Quart. Journ. Geol. Soc.*, 13, 1857, p. 308; and 21, 1865, p. 253. Falconer, *Palaeontological Memoirs*, 2, 1868. H. v. Meyer, *Studien üb. d. Genus Mastodon*, *Palaeontographica*, 1867, 17. Weinsheimer, *Ueber Dinotherium giganteum*, *Palacont. Abh.* 1, 1883, p. 207. Forbes, *Viscera*, *P.Z.S.*, 1879, p. 420. Adams, *Monograph of the British Fossil Elephants*, 3 pts., *Palaeontographical Soc.*, 1877-8. Cope, *The Proboscidea*, *Amer. Nat.*, 23, 1889. Ameghino, *Pyrotherium*, *Bol. Inst. Geograf. Argentino*, 15, 1895, 18, 1897. Lydekker, *Cat. Foss. Mam. B. M.*, 1-5, 1885-7. Andrews, C. W., *Evolution of the Proboscidea*, *Phil. Trans.*, 196, 1904, p. 99.



is used as a prehensile organ ; by means of it the animal conveys food to its mouth, uproots trees, and sucks up fluid, which it may transfer to its mouth or squirt over its body. The ears are large and there is a moderate tail. The tusks are enormously enlarged rootless incisor teeth (*i* 2) and in living forms are only present in the premaxillae. In the mastodon there are also two incisor teeth in the lower jaw which soon fall out in the female, but in the male are retained as tusks. Incisor teeth are also present in the lower jaw of *Dinotherium* where they have the form of tusks, and of *Tetralodon*, *Palaeomastodon* and *Moeritherium*, etc. (see below).

The tusks consist mainly of dentine, being only tipped with enamel in *Elephas* and ridged with the same substance in some extinct species. They are preceded by milk teeth. There are no canines in recent forms. The grinders are highly peculiar. They are enormous elongated teeth with very numerous rows of transversely elongated tubercles forming plates and composed of enamel and dentine. The spaces between these tubercles are in living forms filled with cement, and the grinding surface presents in the worn tooth a number of transverse rhombic marks consisting of dentine with an outer coating of enamel. In the mastodon the cement is sparse, and the dental papillae are short having the form of mamillary prominences (Fig. 294). In *Dinotherium*, *Palaeomastodon*, *Moeritherium*, etc., in which there is the ordinary succession, the molar teeth are bilophodont and tapir-like, and there is no cement on the crowns.\* In *Stegodon* there are six to twelve transverse ridges, the valleys being partly filled with cement. In *Elephas* (Fig. 293) the number of ridges is much greater, increasing in the posterior teeth, so that the last may have as many as twenty-seven. With this increase in complexity, the crowns become longer, so that the brachydont condition of the molars of *Mastodon*, *Dinotherium* and other early forms gives place to a marked hypsodont structure. There are altogether six grinding teeth in modern elephants on each side of each jaw. Of these, three are either premolars which have no predecessors, or deciduous molars which have no successors ; the other three are molars. There are never more than three rarely more than two above the gum at the same time,

\* See pp. 572, 573.



for the posterior teeth, which are larger and have more lamellae than the anterior, only make their appearance after the anterior have been worn down and have fallen out. At first each half of the jaw has only one grinder; behind this a second is soon developed, and so on. The whole series gradually moves forwards in the jaw and, as those in front are worn down and cast off, the posterior teeth are developed and moved forwards into position. In *Dinotherium*, etc., the ordinary succession is found; the milk molars are vertically displaced by premolars and all the grinding teeth are in use at the same time.

The principal peculiarities of the skull (Fig. 292), in addition to the enormous thickness of some of the bones owing to the presence of the air-spaces, are the large size

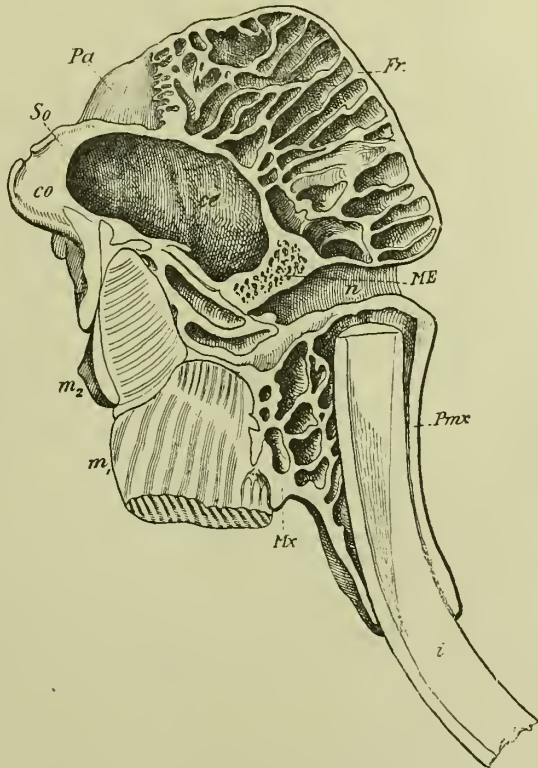


FIG. 292.—Skull of *Elephas indicus* in longitudinal section (from Zittel). So supraoccipital, co occ. condyle, Pa parietal, Fr frontal, Mx maxilla, Pmx premaxilla, ME mesethmoid, n nasal passage, i tusk, m<sup>1</sup>, m<sup>2</sup> first and second grinders.

of the premaxillae which carry the tusks, the shortness of the nasals, in consequence of which the bony nasal passage opens upwards as in whales; the comparatively slender jugal arch, the middle of which only is formed by the jugal, contrary to the arrangement usually found in Ungulates. The mandibles have a high vertical portion and

are extensively ankylosed at the symphysis which forms a kind of spout. In the young the air-cells are but slightly developed, and the great increase in the size of the skull which takes place during growth is mainly due to their development. The lacrymal is small and interorbital. The frontals are produced into supra-orbital processes which give off small postorbital processes. The orbit is not separated from the temporal fossa. There is a broad post-tympanic process which meets the posterior boundary of the glenoid fossa beneath the external auditory meatus. The tympanic is united with the periotic and forms a large rounded bulla. There are no paroccipital or postglenoid processes.

The vertebrae (in *Elephas*) are C 7, D 19-21, L 3-4, S 4, C 26-33. The centra are flattened from before backwards especially in the neck, and the epiphyses remain separate for some time. The scapula has a long backward process from about the middle of the spine (as in some Rodents) and there are no clavicles. The ulna and fibula are complete and separate. The radius is fixed in the prone position, crossing the ulna. The carpalia are successional, and the metacarpals and phalanges are short and thick. The femur is without a third trochanter, the tibia is short, and the fibula articulates with the calcaneum. The astragalus articulates distally with the navicular only, and is remarkable for the flatness of both its surfaces.

The stomach is simple, and the large intestine very long, half the length of the small. The apex of the ventricle is bifid. There is a large caecum and no gall bladder. Primitive features are shown by the presence of two superior venae cavae and by the fact that the cerebellum is left entirely uncovered by the cerebrum. The cerebrum, however, is large and very richly convoluted. The testes remain in the abdomen close to the kidneys, to which they are attached. The vulva is placed on the abdominal surface at some distance in front of the pubis. The uterus is bicornuate and the two mammae are thoracic. The placenta is zonary and the period of gestation is about twenty months, but the time may be variable.\*

Elephants love dark and shady forests. They are purely vegetable feeders, living mainly on the leaves of trees, which they

\* Dr. Chalmers Mitchell informs me that in the case of an Indian elephant in the Zoological Gardens of London, the time appears to have been 28 months, during 23 of which the animal was in the gardens.

frequently uproot for the purpose of getting at the upper leaves. They live to a great age (100 to 120 years, perhaps longer) and are said not to attain maturity till the fortieth year. They are remarkably intelligent and possess a good memory. The two living species are confined to Africa and India (including Ceylon, Burma, Malay Peninsula, Sumatra, Cochin China). Both species have been domesticated, the African more rarely than the Indian. They will rarely breed in captivity.

The Proboscidea constitute a distinct and on the whole isolated order. They are commonly united with the Ungulata. They present features of resemblance to the Rodentia (scapula, etc.) and Sirenia (succession of teeth, etc.), and in many parts of their anatomy are very primitive, e.g. structure of manus and pes, presence of two superior venae cavae, uncovered cerebellum, abdominal testes.

The sirenian affinities have been recently emphasized by Andrews.\* The following characters are common to the two groups: (1) The non-deciduate and zonary placenta, (2) the pectoral mammae, (3) the abdominal testes, (4) the bifid apex of the ventricle, (5) the absence of the condylar foramen always in the Proboscidea and generally in the Sirenia, (6) the bilophodont character of the molars with a tendency to the formation of an additional lobe from the posterior part of the cingulum (talon), (7) the fact that in both groups the molar series move forward in the jaws throughout life, the anterior worn teeth being shed, while fresh teeth come into use behind. There is however no evidence of this last character in the earliest Proboscidea, *Moeritherium* and *Palaeomastodon*.

The Proboscidea are first found fossil in the Middle Eocene of Egypt and a fairly complete series of forms are known connecting the highly specialised modern *Elephas* with the earliest of these remains. Their fossil remains are found in both the Old and the New World.

*Elephas* L. (*Euelephas*),  $i \frac{1}{3} c \frac{0}{3} p$  or  $dm \frac{3}{3} m \frac{3}{3}$ ; the incisors are curved and tipped with enamel; they are usually larger in the male; grinders with numerous laminae. Fossil species are known from the U. Miocene of India, Pliocene and Pleistocene of Eur., Afr., Asia, N. and S. Amer. *E. indicus* L. (distribution, see above), average dental ridge formula 4, 8, 12, 16, 24, laminae of the worn plates nearly parallel, female without tusks, manus with 5, pes with 4 nails, height of full grown male at the shoulder from 8-11 feet. *E. africanus* Blumenb. (*Loxodon*), average ridge formula of molars 3, 6, 7, 7, 8, 10; laminae thicker in the middle, than at the edges (Fig. 293), manus with 4 nails, pes with 3. tusks in both sexes, but smaller in female; larger than the Indian species, a full grown male may measure 12 feet to the shoulder. There are many extinct species, of which may be mentioned the mammoth *E. primigenius* Blu-

\* *Op. cit.*

menb., in the Pleistocene of Eur., As., and Amer. The skin had a thick woolly covering, as is shown by the frozen carcasses occasionally met with in N. Siberia, where the tusks (sometimes from 10-12 feet in length) are found in considerable numbers, affording ivory for export, and also by contemporary drawings scratched on mammoth ivory. The cause of the comparatively recent extinction of the mammoth is doubtful; it may have been due to the decay of the forests in which it lived. *E. meli-tensis* Falcon., a pigmy species found in caves in Malta.

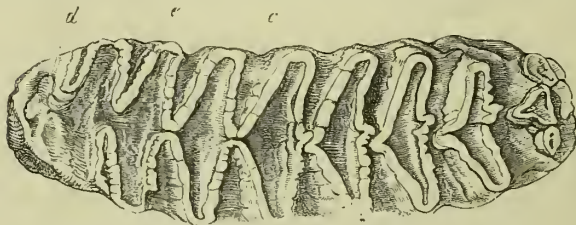


FIG. 293.—Upper molar of *Elephas africanus*. *d* dentine, *e* enamel, *c* cement (from Owen).

Extinct genera, *Stegodon* Falcon., tusks in upper jaw, with enamel band; grinders composed of 6-12 low cusped ridges, with cement in the valleys. Miocene and

Pliocene of Asia. *Dinotherium* Kaup,  $i \frac{1}{4} c \frac{0}{0} p \frac{2}{2} m \frac{3}{3}$ , the grinders being bilophodont (except  $m1$ , which has 3 ridges), and all in function at once, the premolars have milk predecessors; the extremity of the mandible is deflected and the tusks (lower incisors) project downwards (Fig. 295); cranium depressed with but few air-cells: in size it surpassed living elephants; M. and U. Miocene of Eur. and As. *Mastodon* Cuv.,  $i \frac{1}{1 \text{ or } 0} c \frac{0}{0} p \frac{3}{3} m \frac{3}{3}$ ; u. incisors as large tusks with bands of enamel, l. incisors variable, never large, sometimes absent; grinders with mammillated ridges and scanty cement (Fig. 294), the anterior three grinders sometimes replaced, Miocene and Pliocene of Old World, in the New World it survived until the Pleistocene. *Tetrabelodon* Cope, dentition,  $i \frac{1}{4} c \frac{0}{0} p \frac{2}{2} m \frac{3}{3}$ , the upper incisors are tusks and the lower are procumbent teeth in close contact; there appear to have been 3 deciduous molars, the last two of which were replaced; the premolars were shed early; the premolars and molars are brachyodont and bi- or tri- lophodont, the ridges being tuberculated, and  $m3$  has a tuberculated talon; the symphyseal region of the mandible is much elongated. Miocene and Pliocene of Eur. Asia, Afr., N. Amer., extending into the Pleistocene in Amer.

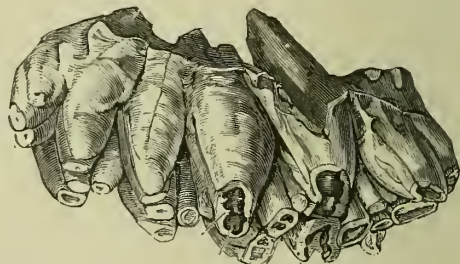


FIG. 294.—Oblique side and crown view of the last upper molar of *Mastodon arvernensis* (from Flower and Lydekker).

*Palaeomastodon* Andrews, from the Upper Eocene of Fayum, Egypt; dentition  $i \frac{1}{4} c \frac{0}{0} p \frac{3}{3} m \frac{3}{3}$ , the upper incisors are tusks, the lower procumbent and spatulate; the premolars and molars very similar to those of *Tetrabelodon* except that all were in use at once in the usual way,



*ml* being most worn; the mandibular symphysis was elongated but not so long as in the last genus, and the basis cranii and facial region of the maxilla longer.

*Moeritherium* Andrews, Middle and Upper Eocene of Fayum; dentition  $i \frac{3}{2}$   $c \frac{1}{0}$   $p \frac{3}{3}$   $m \frac{3}{3}$ ;  $i \ 2$  in the upper jaw is tusk-like though not so large as in the other genera,  $i \ 1$  and  $i \ 3$  are small as is the canine; in the lower jaw  $i \ 2$  is larger than  $i \ 1$ ,  $i \ 3$  being absent; the premolars are cuspidate and the molars bilophodont (quadritubercular). This is the ordinary dentition, save for the absence of  $p \ 1$  in the upper jaw and of  $i \ 3$ ,  $c$  and  $p \ 1$  in the lower. The mandibular symphysis is but slightly elongated.

*Barytherium*  
Andrews, M.  
Eocene.

*Pyrotherium*  
Am., from the  
Cretaceous  
(Eocene) of  
Patagonia has  
been claimed  
as a member  
of this order.

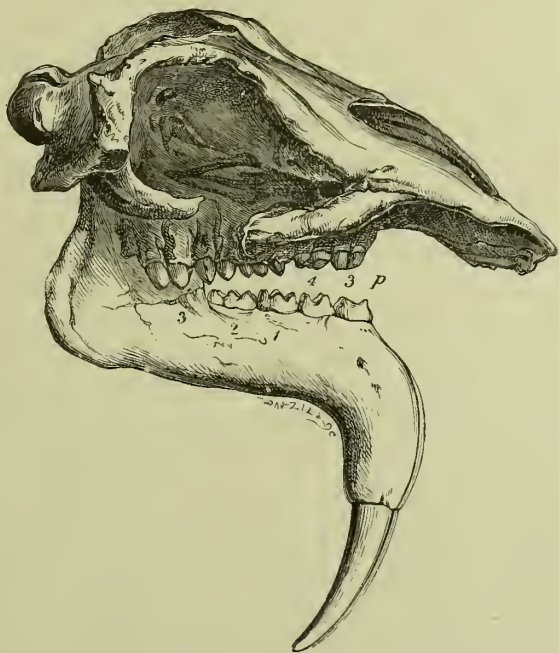


FIG. 295.—Skull of *Dinotherium giganteum*, from the Lower Pliocene (after Kaup, from Flower and Lydekker).  $p \ 3$ ,  $4$  premolars;  $1$ ,  $2$ ,  $3$  molars.

## Order 8. UNGULATA.

Usually hoofed, digitigrade animals in which the digits of the pes never exceed four and the carpal and tarsal bones interlock. There is no os centrale in the carpus and no entepicondylar foramen in the humerus, and clavicles are always absent. The scapula is usually devoid of an acromion. The placenta is diffuse or cotyledonary, the mammae inguinal or abdominal, and the testes always descend into a scrotum.

The Ungulata as thus defined includes the Perissodactyla, and Artiodactyla and excludes absolutely the Proboscidea and



Hyracoidea. This is as it should be, for there are no specially Ungulate features about either of the two latter, and when carefully surveying the facts, it is difficult to understand upon what grounds they have been and are classed with the hoofed animals. But the definition if strictly applied goes further than this and excludes from the Ungulates a certain number of extinct forms, which ought perhaps to be placed with them. Such are the *Lipoterna* (e.g. *Macrauchenia*) which appear to have all the Ungulate characters mentioned except the interlocking carpals and tarsals and the universal absence of digit No. 5 on the pes. It is true that this group has some remarkable characters of its own, but in the present state of knowledge it may fairly be left with the Ungulata. A case might also be made out for including the Toxodontia and the Amblypoda, but after careful consideration they must, we think, be excluded. It is true that both these groups present some of the ungulate features, but they are without the others, and they both present remarkable features of their own, which, we feel convinced, would exclude them from the group were they alive at the present day so that we could study their soft parts. We refer especially to the structure of the brain as revealed by casts of their skulls.

There remain the Typotheria, Ancylopoda and the Condylarthra. These are dealt with fully below. Here it is only necessary to say that the two latter, though showing some ungulate features depart far too widely from that type to be included with it in classification; and that the Typotheria differ from the Ungulata in all their characters.

In maintaining these opinions as to the limitations of the order Ungulata, we are in opposition to the views of many eminent zoologists, men who have devoted much thought, labour and research to the study of these obscure remains. We therefore urge our views with much diffidence and have only decided to give expression to them after considerable hesitation. But we feel that we cannot evade the matter in a treatise of this kind. We are obliged to look into the facts and in forming a judgment upon them we must exclude from our minds as far as is possible all that bias which comes so readily from theoretical predilections.

**Dentition.\*** The back teeth are nearly always rooted and may

\* See pp. 499-508.

be either *bunodont* (p. 504), or *lophodont* (p. 504). *Selenodont* teeth are a variety of the *lophodont* type in which the tubercles have a crescentic form; they are found mainly in the ruminant division of the Artiodactyla. As a general rule the teeth have short crowns and the neck of the tooth, i.e. the junction of the crown and root lies at the top of the alveolus (*brachyodont*); but in Equidae and some ruminant artiodactyls the crowns are much lengthened and the neck of the tooth lies for some time in the socket (*hypsodont* or *hypsodont*, p. 505). The *hypsodont* tooth is clearly more adapted for prolonged use; there is more wear in it and its possessor is able to eat habitually drier and harder food than creatures possessing *brachyodont* grinders. The layers of hard enamel traversing the softer dentine and cement give rise to a slight roughness of the surface which is of advantage for trituration of the food.

There is considerable modification of the manus and pes within the group, more so than perhaps in any other organ; and as these modifications are combined with the ungulate characters and are continuous or nearly so, i.e. the extreme modifications are connected by intermediate gradations throughout the group, there is comparatively little difficulty in fixing the systematic position of their possessors. To begin with, we may describe a constant character which is found in all ungulates and which is mentioned in the definition. The bones of the two rows of the carpus and tarsus are not placed vertically below one another, are not *serial* or *successional* as it is called, as they are in most mammals, e.g. the elephant or *Hyrax* (Fig. 290), but the bones of the distal row have been shifted towards the inner side, so that in the carpus the os magnum is partly under the scaphoid as well as under the lunar, and the unciform articulates not only with the cuneiform but also with the lunar (Fig. 298). In the pes the astragalus no longer articulates solely with the navicular but it also has a surface of articulation for the cuboid (Fig. 299). In this condition which is, as we have stated, characteristic of ungulates, the two rows of carpal and tarsal bones are said to interlock, and the interlocking gives greater strength to the carpal and tarsal joints.

The modifications in the manus and pes relate to the number of digits present. In the manus the greatest number of complete digits is four with occasionally a trace of the pollex, in the pes

four with never a trace of the hallux. The absence of digit No. 1 may be therefore taken as a characteristic of the group. In the Suidae and Hippopotamidae, there are four digits in each foot, but digits Nos. 2 and 5 are weaker than the others and may not reach the ground. This change is accompanied by an elongation of the metacarpals and metatarsals, *metapodia* as they are called. In the *Ruminantia* the outer digits are very small and functionless as in the deer (Fig. 308) or entirely absent as in *Camelidae* and some *Bovidae*, and the metapodia of the persisting large digits (Nos. 3 and 4) are united into the so-called *cannon bone*. In the *Perissodactyla* the modifications are slightly different. Here in the tapir the manus has four complete digits (No. 1 being absent), the pes three (Nos. 1 and 5 being absent); the rhinoceros has three in both limbs, while the horse has only one complete digit (No. 3) with traces of the metacarpals of digits 2 and 4. In this sub-order digit No. 3 is larger than the others even in the tetradactyle tapir (Fig. 309). The gradual elongation of the metapodia is also manifest in this series as may be gathered from an inspection of the figures (Fig. 316). The Ungulata are found all over the world except the Australasian region. They are almost all herbivorous and none purely carnivorous. The forms with broad tetradactyle feet frequent places where the ground is soft (rhinoceros, hippopotamus); they may be described as almost semiplantigrade, for although they stand on their digits the weight is partly borne by a large pad on the hinder side of the foot. The majority, however, are purely digitigrade, and walk on the tips of their reduced toes which are encased in hoofs. These creatures inhabit hard ground, grassy plains and mountain sides and are swift and active runners.

There are three suborders, the *Artiodactyla*, the *Perissodactyla*, and the *Lipoterna*.

#### Sub-order 1. ARTIODACTYLA.\*

Digitigrade forms in which the axis of the limbs passes between digits Nos. 3 and 4, these digits being symmetrical with each other and their metapodia closely applied together or united into a cannon bone. The premolars and molars are not alike and the last lower molar is three-lobed. The first milk molar is not

\* W. Kowalevsky, *Palaeontographica*, 22, 1873-4. E. D. Cope, The *Artiodactyla*, *Amer. Naturalist*, 22 and 23, 1888-9.

replaced; it may persist for some time. There is no alisphenoid canal and the nasals are not expanded posteriorly. The number of dorso-lumbar vertebrae is always nineteen. The femur is without a third trochanter, the fibula articulates with the calcaneum, and the facets upon the distal face of the astragalus for the navicular and cuboid are sub-equal, and both its distal and proximal surface are pulley-like.

These are the differential characters of the living members of the sub-order, and it is upon their application to the imperfectly known extinct forms that the systematic position of these must depend. The digits are very commonly reduced in number; the limit of the reduction being found in the more specialised Ruminants in which digits 3 and 4 alone persist, all trace of the others having disappeared.

The dentition consists typically of 44 teeth,  $i \frac{3}{3} c \frac{1}{1} p \frac{4}{4} m \frac{3}{3}$ , but there is a tendency towards the suppression of the upper incisors, and, as already stated, the first tooth of the premolar series is probably the long-persistent first milk molar. The premolars are usually simpler than the molars (Fig. 296).

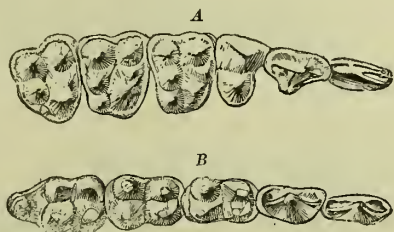


FIG. 296.—*Homacodon vagans*. A right upper premolars 2-4, molars 1-3; B right lower premolars 3 & 4, molars 1-3 (after Marsh, from Woodward).

In the so-called primitive forms the grinding teeth are low-crowned (brachyodont) and the tubercles are conical (bunodont); the latter being in two pairs (Fig. 296) with a tendency to the intercalation of an accessory tubercle in the upper molars between the tubercles of either the anterior or the posterior pair. There is almost always a heel (talon) on the last molar of the lower jaw (Fig. 296 B). In many forms the tubercles become V-shaped or semilunar and are connected by basal ridges; in this way the teeth pass through a stage which may be called buno-lophodont or buno-selenodont to selenodont, the form which is eminently characteristic of the Ruminantia (Fig. 297). In selenodont forms the concavity of the semilunar tubercles are directed outwards in the upper and inwards in the lower jaw; and in the upper jaw the two outer tubercles are usually united, forming the outer wall of the tooth, and there is a projecting ridge along the wall at the

point of union. In the lower molars the inner tubercles usually unite to form an inner wall. The lower molars are usually narrower than the upper.

The tubercles are generally short (brachyodont) but in the higher forms they lengthen and the spaces between them become filled in with cement. In some of the ruminants (*Bovidae*) the crowns become as long as in the Perissodactyla : this is the hypsodont condition.

The skull in the primitive extinct forms recalls that of the *Carnivora*. In the higher forms the face becomes lengthened. The lacrymals extend on to the face.

In the more primitive forms the odontoid process is conical ; with increased specialisation it tends to become spout-shaped.

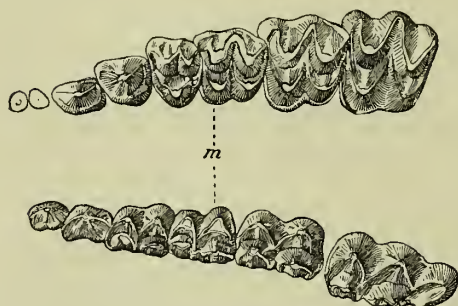


FIG. 297.—Selenodont dentition of an Oreodont *Agriocherus latifrons*. The upper teeth are above in the figure (after Scott from Zittel). *m* first molar.

But this as in the case of *Agriocherus* (p. 585) does not always hold. In the hinder dorsal and in the lumbar vertebrae the prezygapophysis frequently bends round the postzygapophysis of the preceding vertebra, so as to overlap and articulate with its dorsal

surface. The scapula is generally without an acromion.

The ulna and fibula are complete and distinct in some forms, but there is a tendency to their reduction and fusion with the radius and fibula. In the ruminants the fibula is only represented by its lower end (mallolar bone), which articulates with the calcaneum. As already stated the digits tend to diminish in number. There are five metacarpals in the *Oreodontidae* (Fig. 297 bis, *A*) and *Anoplotheridae*, but No. 1 is reduced. In all others this digit has completely gone, but digits 2 and 5 generally persist though reduced. Digits 3 and 4 always persist and in the higher forms their metapodia are united into a cannon bone which is generally grooved in front or slightly cleft below and always contains two medullary cavities.

In the artiodactyl manus with five metacarpals metacarpal 1



articulates with the trapezium, mc. 2 with the trapezium, trapezoid, and magnum, mc. 3 with the magnum and unciform, mc. 4 and 5 with the unciform (Fig. 297 bis, *A*). If this arrangement is maintained with reduction in the digits, the reduction is spoken of as inadaptive reduction (297 bis, *B*); inadaptive reduction is characteristic of the ancient forms. In adaptive reduction the upper articulating surfaces of mc. 3 and 4 broaden out and push the lateral metapodia outwards, so

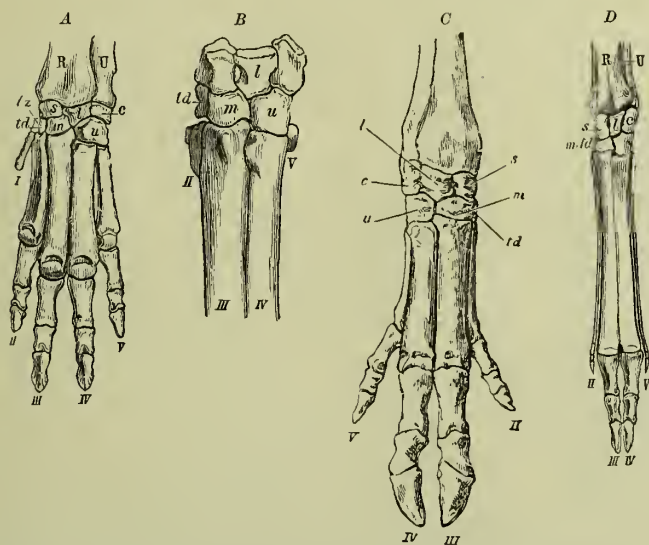


FIG. 297 bis.—Manus *A* of *Oreodon*, *B* of *Xiphodon*, showing inadaptive reduction; *C* of *Sus*, *D* of *Tragulus*, showing adaptive reduction (from Zittel). *c* cuneiform; *l* lunar; *m* magnum; *R* radius; *s* scaphoid; *td* trapezoid; *tz* trapezium; *U* ulna; *u* unciform; *i-v* digits numbered.

that mc. 2 ceases to articulate with the magnum (Fig 297 bis, *C*, *D*). The pes is always ahead of the manus in reduction and in the fusion of the metapodia. It never possesses even the metatarsal of digit 1.

It is said that the metapodia when fused in the adult retain their distinctness in the embryo, thus corresponding with the older forms. But it must not be forgotten (1) that this distinctness is confined to the stage of cartilage, (2) that the metapodia, however close the coalescence may be, always show distinct traces of their double origin in the adult (separate medullary cavities, and grooved surface), and (3) that no traces of the

skeletal parts of digits which are totally missing in the adult have so far been discovered in the embryo.

The stomach is generally complex, the caecum small, the placenta diffused or cotyledonary. The mammae are few and inguinal or numerous and abdominal.

The Artiodactyla constitute by far the largest group of living Ungulates. They are rich in genera and species and they are found all over the world except in Australia and New Zealand. The living forms are divisible into quite well defined groups, but

there are a large number of extinct forms, which tend to fill up the gaps between existing families and to obliterate the dividing lines. The earliest of these are found in the Eocene.

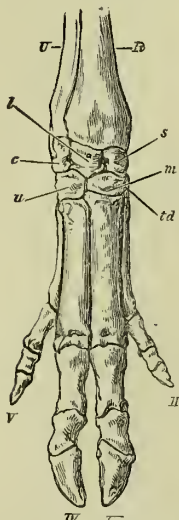


FIG. 298.

FIG. 298.—Bones of the manus of the pig (*Sus scrofa*)  $\times \frac{1}{2}$  (from Flower), digits numbered, bones with initial letters.

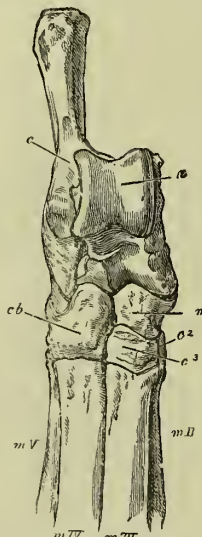


FIG. 299.

FIG. 299.—Right tarsus of pig  $\times \frac{1}{2}$ .

and 5 do not reach the ground in walking. The metacarpals and metatarsals are generally separate and never completely fused together. The axis of the face is bent upon the basi-cranial axis; the orbit is not closed behind, the postorbital processes of the frontal and jugal not meeting; the openings of the lacrymal canal are on the face; the nasals are long and the premaxillae unite with them for some distance; there is often a prenasal bone; the bulla is large, the bony auditory meatus is long; the post-glenoid and post-tympanic processes of the squamosal are united beneath the meatus, and there is a long par-occipital process. The centra of the cervical vertebrae are short. The

\* H. v. Nathusius, *Die Racen des Schweines*, 1860, and *Vorstudien für Geschichte u. Zucht der Hausthiere*, Berlin, 1864. Marsh, *Homacodon*, *Amer. Journ. Sci.* (3), 48, 1894, p. 261. Filhol, *Listriodon*, *Bibl. École Hautes Études*, 37, 1890, p. 205.

ulna and fibula are complete and separate from the radius and tibia. There is a single precava. The stomach is fairly simple, with a cardiac pouch and a groove leading towards the pylorus from the oesophageal opening. There is a caecum. The placenta is diffuse, the teats are abdominal and the testes descend into a scrotum. Living forms are confined to the Old World. † Fossil remains are first found in the Eocene of Europe and N. America. *Sus* L., milk dentition  $i \frac{3}{3} c \frac{1}{1} m \frac{4}{4}$ ; permanent dentition  $i \frac{3}{3} c \frac{1}{1} p \frac{3}{3} m \frac{3}{3}$ ; the canines have persistent roots and project as tusks, less developed in the female; gestation 16–20 weeks; palaeartic and oriental regions, in other regions introduced by man; *S. scrofa* L., wild boar, with many varieties; the source of the various breeds of domestic pig is unknown; *S. salvanius* Hodg., no larger than a hare, India; 13 other species are distinguished and many extinct from the Miocene onwards. *Potamochoerus* Gray, river-hogs, Africa and Madagascar. *Babirussa* Less.,  $i \frac{2}{2}$

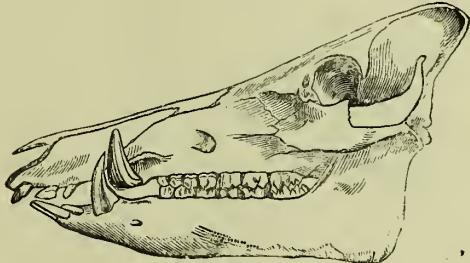


FIG. 300.—Skull of *Sus scrofa ferus*.

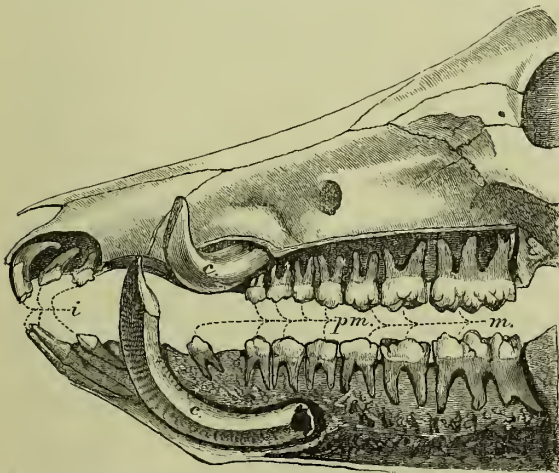


FIG. 301. Left side view of dentition of the boar (*Sus scrofa*), showing roots exposed (from Flower and Lydekker). *i* incisors, *c* canines, *pm* premolars, *m* molars.

$c \frac{1}{1} p \frac{2}{2} m \frac{3}{3}$ , enormous canines in the male, the upper piercing the skin, almost hairless, 1 species, Celebes and Buru. *Phacochoerus* G. Cuv., wart-hogs, with large cutaneous lobes on each side of the face,  $i \frac{1}{1} c \frac{1}{1} p \frac{2}{2} m \frac{3}{3}$ ; teeth tend to disappear with age except the canines and posterior molars, which latter attain an enormous development, owing to

the great number and elongation of the tubercles; the form of the last molars and the fact that the anterior grinders are gradually worn down and disappear, leaving the last only, constitutes an approximation to the condition in elephants; 2 sp., Africa. The following extinct genera, many tending to connect the Suidae and Dicotylidae, are placed with the Suidae; some of them show affinities outside these

families: *Achaenodon* Cope; *Homacodon* Marsh (*Pantolestes*), Middle Eocene, N. Amer., Bridger Beds.; *Choeropotamus* Cuv.; *Palaeochoerus* Pomel; *Listriodon* Meyer, the cusps of the upper and lower molars fuse

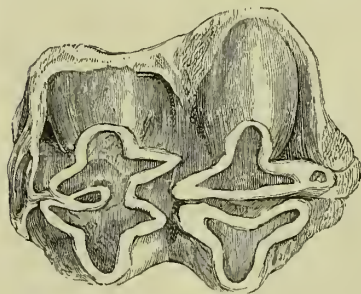


FIG. 302.—Grinding surface of a worn molar of *Hippopotamus amphibius* (from Flower and Lydekker, after Owen).

into complete transverse ridges, Middle Miocene. *Elothierium* \* Pomel, Eocene and Miocene of Europe and America, with completely enclosed orbit, with two complete toes, digits 2 and 5 being represented only by their metapodia, last molar without a supplementary lobe.

Fam. 2. **Dicotylidae.** Peccaries  $i \frac{3}{3} c \frac{1}{1} p \frac{3}{3} m \frac{3}{3}$ , upper canines directed outwards, the last premolar nearly as complex as the molars, only three toes on pes; stomach 3-chambered with oesophageal groove; the metacarpals

and metatarsals of digits 2 and 3 coalesce into a cannon bone, on the back is an oleaginous musk gland; only 2 young at a birth; 2 species, New World, from Texas to Patagonia. Many extinct species Pliocene and Pleistocene of Amer.

Fam. 3. **Hippopotamidae.**† Skin almost hairless; with huge head and large heavy unwieldy body with a thick skin, with short tetradactyle limbs all the digits of which rest on the ground and have nail-like hoofs; milk dentition  $i \frac{3}{3} c \frac{1}{1} m \frac{1}{1}$ , permanent,  $i \frac{2}{2} c \frac{1}{1} p \frac{3}{3} m \frac{3}{3}$ , premolars simpler than molars; molars with four tubercles which wear down so as to present a double trefoil pattern (Fig. 302); last lower molar trilobed. Incisors tusk-like, rootless; canines large, curved, rootless. The orbits are tubular and nearly completely enclosed; tympanic large and ankylosed with the approximated post-tympanic and postglenoid processes of the squamosal. Scapula with a short acromion, ulna and fibula complete. Brain not richly convoluted. Stomach very large, with three compartments. No caecum. Kidneys lobulated. Mammae inguinal. Scrotum absent. Herbivorous, semiaquatic; confined to Africa. *H<sup>hippopotamus</sup> amphibius* attains a weight of four tons, Africa; *H.*

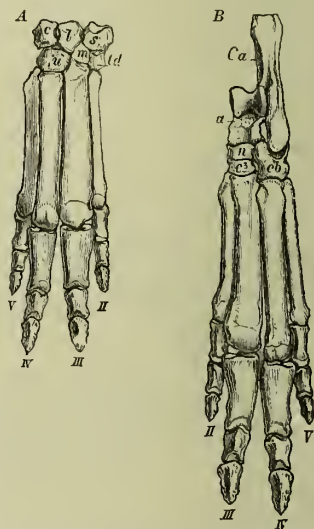


FIG. 303.—*Hyopotamus (Ancodus) velatus* Cuv., Oligocene. *A* anterior, *B* posterior foot  $\times \frac{1}{2}$ . digits numbered, carpals and tarsals marked by initial letters (after Kowalevsky, from Zittel).

\* Kowalevsky, *Palaeontographica*, 22, 1876. Marsh, *Amer. Journ. of Science* (3), 48, 1894, p. 407.

† Falconer, *Palaeontological Memoirs*, 1 and 2, London, 1868. Lydekker, *Indian Tertiary and Post Tertiary Vertebrata, Palacont. Indica*, ser. 10, 1-4, 1874-87. Filhol, *Ann. Sci. Nat.* (7), 16, 1893, p. 151.

\*) *Xicotyles* Cuv.



*liberiensis* is a small species with only two incisors in the lower jaw, Liberia (formerly called *choeropsis*); extinct species from all over the Old World, including Madagascar (not in Australia), Pliocene and Pleistocene.

All the above families have tuberculated molars.

We now come to a number of extinct forms in which the tubercles of the molars are connected by low ridges, so that they may be called bunolophodont. They are intermediate forms leading to the Ruminantia. The Caenotheriidae and Xiphodontidae show affinities to living groups. The others though intermediate between Suidae and Ruminantia show no special affinity to any living group.

Fam. 4. **Anthracotheriidae**.\* Extinct forms, Eocene and Miocene.

$i \frac{3}{3}$   $c \frac{1}{1}$   $p \frac{4}{4}$   $m \frac{3}{3}$ ; u. molars with 4 tubercles and an intermediate tubercle in the anterior

half of the tooth, molars tending to selenodonty; tetradactyle limbs, inner and outer toes rather smaller than the middle, metacarpals and

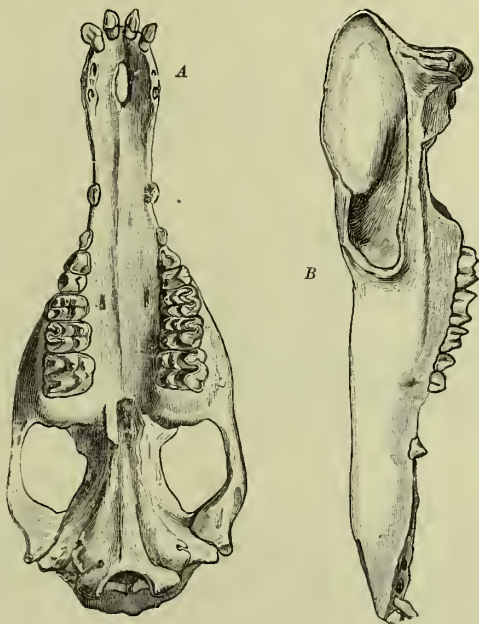


FIG. 304.—*Hyopotamus velauvus* Cuv. Skull, A from below. B from the side (after Kowalevsky, from Zittel).



FIG. 304 bis.—*Anoplotherium latipes* Gerv., Upper Eocene. A the two hinder upper pre-molars and the anterior molar. B the two hinder lower molars. The cusps are lettered as follows:  $a$  antero-external,  $b$  antero-internal,  $b^1$  antero-intermediate,  $c$  postero-external,  $d$  postero-internal;  $\alpha$  antero-internal,  $\beta$  antero-external,  $\gamma$  postero-external;  $\beta'$ ,  $\beta''$ ,  $\gamma'$  the three inner tubercles (nat. size, from Zittel).

metatarsals not fused (Fig. 303); ungual phalanges pointed. *Anthracotherium* Cuv., *Hyopotamus* Ow. (*Ancodus* Pomel), *Merycopotamus* Falconer, u. molars with 4 tubercles only.

Fam. 5. **Anoplotheriidae**.† Extinct, Eocene and Miocene;  $i \frac{3}{3}$   $c \frac{1}{1}$   $p \frac{4}{4}$   $m \frac{3}{3}$ ; teeth in a continuous row, without gaps as in man; molars seleno-bunodont, u. molars with an intermediate tubercle (Fig. 304 bis, A, b)

\* W. Kowalevsky, On the Osteology of the Hyopotamidae, *Phil. Trans.*, 1873. † Cuvier, *Ossém. Foss.*, 3, 1812.



sometimes between the anterior and sometimes between the posterior tubercles; anterior premolars elongated and cutting (Fig. 305); feet with 4, 3, or 2 digits, reduction inadapative (Fig. 305, D), metacarpals and metatarsals not united; ungual phalanges pointed. *Anoplotherium* Cuv., with

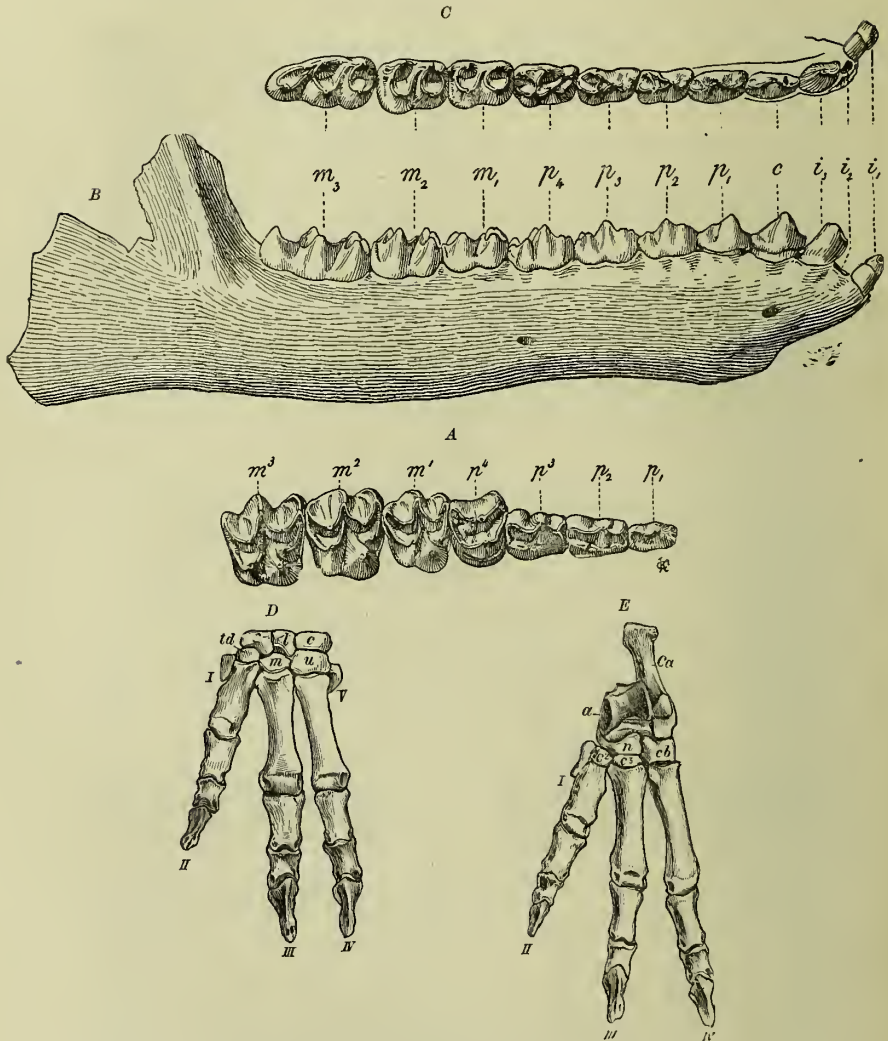


FIG. 305.—A Upper grinders, B right lower jaw from the side, C the same from below, D manus, E pes of *Diplobune quereyi* Filhol (from Zittel).

long tail, with three complete digits (probably webbed); Eocene of Europe. *Diplobune* Rüt.

Fam. 6. **Caenotheriidae**.\* Small animals with selenodont dentition, with 4 complete digits, outer digits not reaching ground, radius and ulna separate; they are supposed to show affinities to the Tylopoda; Miocene, France. *Caenotherium* Brav., *Plesiomeryx* Gervais. *Dichobune* Cuv., U. Eocene, Europe, with tubercular molars is allied here.

Fam. 7. **Xiphodontidae**.† With selenodont molars, feet slender, didactyle, the lateral metacarpals and metatarsals much reduced, reduction madaptive. Teeth continuous, without gap, canine not enlarged; last premolars like the molars; appear to be related to the Tragulidae and Cervidae, U. Eocene, Europe. *Xiphodon* Cuv., *Dichodon* Ow., *Amphimeryx* Pomet.

Fam. 8. **Oreodontidae**.‡ Teeth in closed series or with diastema, molars selenodont, u. molars with 4 rarely with 5 crescents, lower canine incisor-like, and anterior premolar assuming its function; metacarpals and metatarsals separate. Feet tetradactyle, manus sometimes pentadactyle. U. Eocene to L. Pliocene of N. America. They are closely allied to the Anthracotheriidae and Anoplotheriidae, but not to any living forms. *Protoreodon* Scott and Osb., *Oreodon* Leidy, dentition complete, without diastema, orbit complete, odontoid spoutshaped, said to have had a clavicle. *Agrichoerus* Leidy, premaxillae toothless, diastema in both jaws, manus with 5, pes with 4 digits, apparently ending in claws, § pollex, which is small and functionless, apparently occupies an opposable position.

#### Ruminantia.||

Living selenodont Artiodactyls with complicated stomach; usually without incisors in the upper jaw, or with only one pair; three pairs of incisors in lower jaw with an incisiform canine applied to them;  $p \frac{3}{4} m \frac{3}{4}$ ; metapodia 3 and 4 always united to a cannon bone (metacarpals remain long separate in *Hyomasthus*). Digits 2 and 5 always reduced and frequently absent; horns provided with a bony core generally present. The stomach of a typical ruminant (Fig. 306) is divided into four chambers, of which two—the rumen and reticulum—may be regarded as belonging to the cardiac, and two—the psalterium and abomasum—to the pyloric division. The rumen or paunch is a large sac on the cardiac side with a papillated lining. It opens by a wide aperture into the smaller reticulum the lining of which is raised into a number of folds which bound small hexagonal cells. The reticulum opens into the psalterium which is part of the pyloric division; it is tubular and its lining is produced into a number of longitudinal lammelliform folds, which bear some resemblance to the leaves of a book (hence the name). The fourth chamber is the abomasum or rennet-stomach; it has a vascular glandular lining and is the digestive chamber of the stomach. The oesophagus opens at the junction of the paunch and the reticulum and there is a groove bounded by muscular

\* Filhol, *Ann. Sci. Geol.*, 8, 1877 and 10, 1879. Owen, *Palaeontology*, 1860. Lydekker, *Cat. of the Foss. Mam. in the B.M.* 1885-7.

† Cuvier, *Ossem. Foss.*, 3, 1812.

‡ Scott, *Morph. Jahrb.*, 16, 1890, p. 319.

§ Wortman, *Bull. Amer. Mus. N. Hist.*, 7, 1895, p. 145. In spite of this remarkable feature, the animal appears to have been digitigrade.

|| Rüttimeyer, *Fauna der Pfahlbauten*. Id., Versuch einer natürlichen Geschichte des Rindes, *Denksch. der Schweizer Naturf. Gesellschaft*, 22 and 23. Sundevall *Methodische Übers. üb. d. wiederkauenden Thiere*, 2 Theale, 1847.

folds leading from it to the psalterium. The lips of these folds can be approximated so as to convert the groove into a canal leading from the oesophagus to the psalterium. The food when first swallowed passes into the rumen and reticulum and remains there, mixed with swallowed saliva until the animal has eaten what it requires. It then lies down to chew the cud or ruminate. The first part of this process is akin to vomiting, portions of the swallowed food being successively regurgitated into the mouth, by a contraction of the diaphragm and abdominal muscles and a reversed peristalsis of the oesophageal muscles. In the mouth it is thoroughly masticated and then again swallowed. But now the finely triturated food does not stay in the paunch but passing along the groove, the lips of which may be approximated, it enters the psalterium through which it passes into the abomasum, where it is submitted to the action of the gastric juices. In the Tragulidae and the Camelidae the stomach is very similar in its main features, but the psalterium is reduced or absent. The placenta is generally cotyledonary, i.e. the villi of the chorion are concentrated into a number of bunches or cotyledons, the intermediate portions being devoid of papillae.

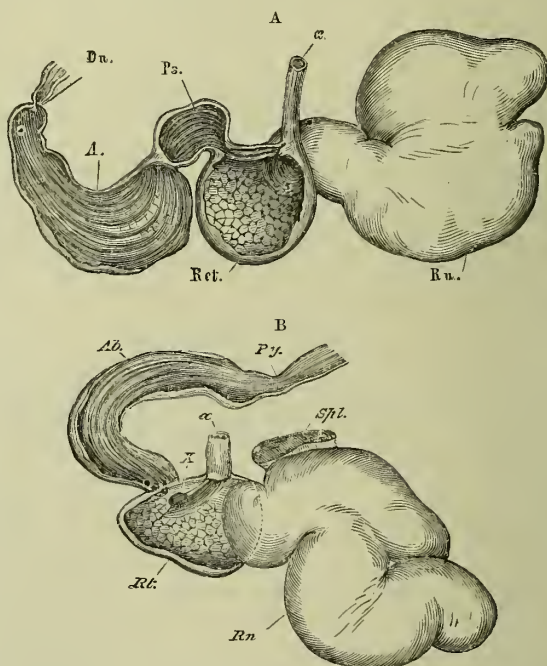


FIG. 306.—A stomach of a sheep, B of *Tragulus*. *oe* oesophagus, *Ru* rumen, *Ret* reticulum, *Ps* psalterium, *A*, *Ab* abomasum, *Du* duodenum, *Py* pylorus (from Huxley).

ledonary, i.e. the villi of the chorion are concentrated into a number of bunches or cotyledons, the intermediate portions being devoid of papillae.

The Ruminantia comprise the Camelidae, Tragulidae, and Pecora.

Fam. 9. **Camelidae (Tylopoda).** Without horns;  $i \frac{3 \text{ to } 1}{3}$   $c \frac{1}{1}$   $p \frac{4 \text{ to } 2}{4 \text{ to } 1}$   $m \frac{3}{3}$ ; the dentition is complete in some of the extinct, but reduced in the living; grinders selenodont, hypsodont. Arches of the cervical vertebrae perforated by the vertebralarterial canal as in *Macrauchenidae*; orbit enclosed, tympanic bullae filled with spongy bone. Ulna reduced and ankylosed to radius, fibula represented only by its distal end, the malleolar bone, which is articulated to the lower end of the tibia and to the calcaneum. Trapezoid and magnum, cuboid and navicular distinct, cuneiforms 2 and 3 fused; feet tetra- or didactyle, outer toes absent in recent

forms; metacarpals and metatarsals 2 and 3 fused except in the oldest forms; cannon bone cleft below, digits with nails not hoofs, digitigrade on cushion-like pads. Stomach 3-chambered, psalterium absent, rumen smooth, with a number of diverticula with narrow openings which can be shut off by a sphincter muscle from the stomach: these are the water-cells and into them can pass the fluid of the stomach. The blood corpuscles are elliptical. Placenta diffuse. Two living genera, *Camelus* L., camels and dromedaries, dentition  $i \frac{1}{3} c \frac{1}{1} p \frac{3}{2} m \frac{3}{3}$ , three incisors in upper jaw in the young; lower incisors procumbent; with one or two dorsal adipose humps; hairy not woolly, 2 species, Asia; *C. dromedarius* L., arabian camel, one hump; unknown in the wild state; *C. bactrianus* L., 2 humps, also domesticated but wild in Turkestan. Fossil species in U. Miocene of India. *Lama* (*Auchenia*) G. Cuv., dentition  $i \frac{1}{3} c \frac{1}{1} p \frac{2}{2 \text{ or } 1} m \frac{3}{3}$ ; without hump, hair woolly, smaller than *Camelus*, they kick, bite, and spit, and in their stomach are found bezoar stones; 4 species usually distinguished, *L. glama*, the lama (not known in the wild state); *L. pacos*, the alpaca; *L. huanacus*, the guanaco, *L. vicugna*, the vicugna; all in S. America, the two first domesticated. Extinct species from Pliocene and Pleistocene of Amer. Extinct genera from the Miocene onwards of Amer. In *Leptotragulus* Scott and Osb., from the Eocene of Amer. with 3 premolars only in the lower jaw, there are 4 toes and the metapodia are separate. *Protylopus* Wortm.,\* Eocene, N. Amer., dentition complete, orbit not enclosed, pes with digits 2 and 5 vestigial, about the size of a rabbit. *Poebrotherium* † Leidy, Miocene of N. Amer., in form and size resembling a small gazelle, has brachyodont, complete dentition,  $i \frac{3}{3} c \frac{1}{1} p \frac{1}{4} m \frac{3}{3}$ , metapodials separate and remnants of metapodials 2 and 5. *Protolabis*, Miocene, dentition as in the last. *Procamelus* Leidy, Miocene and L. Pliocene of N. Amer.  $i \frac{1}{3} c \frac{1}{1} p \frac{1}{4} m \frac{3}{3}$ , metapodia united and no trace of lateral digits. No fossils of the *Camelidae* except those of the genus *Camelus* have been found in the Old World. It has been held that the extinct genera show less and less specialisation as *Camelidae*, the older they are; but this statement is only a rough approximation to the facts. *Leptotragulus* ‡ (*Parameryx*) which is found in the same beds as *Protylopus* and has more complete outer digits, has a dentition more specialised not only than that of *Protylopus* but even than that of the later *Protolabis*, in the fact that there are only 3 lower premolars. Wortman (*op. cit.*) in his account of the phylogeny of the *Camelidae* gets over this fact by describing *Leptotragulus* as a "precociously specialised side branch which died out at the close of the Eocene." Moreover *Protylopus*, which by its small size and other features might be regarded as a primitive type, possesses unfortunately hardly any trace of the outer digits in the pes. This difficulty is got over by supposing that the manus, which is unknown, possessed four digits (Wortman, *op. cit.*, p. 137).

Fam. 10. **Tragulidae**,§ Chevrotains. Hornless small animals, with conical odontoid process, four complete toes (outer toes reduced), metapodia of 3 and 4 uniting late, complete fibula ankylosed at its lower end with the tibia, well developed canines, secant premolars, three-chambered stomach and diffuse placenta. The premaxillae are edentulous, the lower

\* J. L. Wortman, The Extinct Camelidae of N. America, etc., *Bull. Amer. Mus.*, 10, 1898, p. 93-142.

† Scott, *Journ. Morph.*, 5, 1891, p. 1.

‡ Scott, *Trans. Amer. Phil. Soc.*, N.S., 16, 1896, p. 479.

§ Thomas, *P.Z.S.*, 1891, p. 385.



canines are incisiform,  $p \frac{3}{3} m \frac{3}{3}$ , the premolars secant; molars selenodont; the navicular, cuboid and ectocuneiform bones are united. The psalterium of the stomach is reduced to a tube. Blood corpuscles  $\frac{1}{10000}$  in. in diameter. 2 living genera, S. Asia and Africa; an ancient family, known since the Eocene. They are in many respects intermediate between the Ruminants and the other Artiodactyls, the stomach, placenta and feet recalling the latter. *Tragulus* Pall., smallest living Ungulate, 3 species from the Malay Peninsula, 1 from Ceylon and India, 1 species in the Pliocene. *Hyomoschus* Gray (*Dorcatherium*), 1 species, the water-chevrotain, from W. Africa. Extinct genera, *Lophiomeryx* Pomel, Eocene, France; *Gelocus* Aymard, Miocene, France, sometimes placed with the *Xiphodontidae*; *Dorcatherium* Kaup, Miocene, Europe and Asia.

### Pecora (Cotylophora).\*

Skull usually with horns containing a bony core  $i \frac{0}{2} c \frac{1 \text{ or } 0}{1} p \frac{3}{3} m \frac{3}{3}$ ; lower canines as incisors; premolars simpler than molars; odontoid process crescent-shaped; molars brachydont or hypsodont; with closed orbit; a vacuity between the nasal, lacrymal, frontal and maxilla (absent

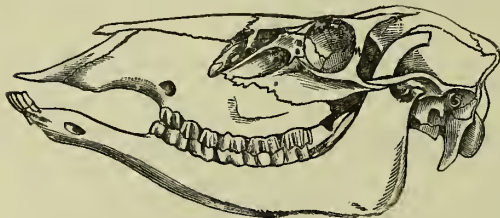


FIG. 307.—Skull of *Cervus canadensis*.

in sheep and oxen); large lacrymals, often with a depression, the suborbital or lacrymal fossa; tympanic not fused to periotic; bulla small without cancellous tissue; large paroccipital process. Ulna reduced, fixed behind the radius;

fibula reduced to the malleolar bone which articulates with the lower end of the tibia; metapodia of digits 3 and 4 ankylosed into a cannon bone, those of 2 and 5 never complete and often absent together with the reduced digits; navicular and cuboid coalesced. The stomach has four complete chambers. The placenta is cotyledonary. The Pecora are entirely absent from the Australian region, and there are comparatively few living forms in the New World. Bovidae are entirely absent from the Neotropical region and there are only four genera in the Nearctic. Living Cervidae are entirely absent from the Ethiopian region.

Fam 11. *Cervidae*.† Deer. Horns when present have the form of antlers. They consist of bony processes of the frontal bones covered during their growth by a soft vascular velvety skin. They are found in the male only, but in the reindeer they occur in both sexes. They are absent altogether only in *Moschus* and *Hydropotes*. They are shed each year after the rutting season and grow again with great rapidity in the following year. When they have attained their full size a circular ridge—the *burr*—is formed round the base at a short distance from the skull, and the 'velvet' gradually dries up and is rubbed off. Later absorption of bone takes place on the proximal side of the burr and the antler is shed.

\* A. H. Garrod, *Proc. Zool. Soc.* 1877, p. 2.

† Rütimcyer, *Beitr. Nat. Geschichte d. Hirsche*, *Abh. Schweiz. paläont. Ges.* 7, 1880; 8, 1881; 10, 1883. Lydekker, *Deer and their Horns*, 1898.



There are no horns in the young, but they make their appearance in the first year in a simple form, becoming, in the species which have branched antlers, more complicated and branched at each subsequent year until complete maturity is attained. The main stem of the antler beyond the burr is called the *beam*; the part below the burr is the *pedicle*; the branches of the beam are called the *tines* or *snags*. The teeth are brachyodont, the neck being from the first on a level with the alveolar border. Upper canines are usually present in both sexes. The magnum and trapezoid are fused, as are usually cuneiform 2 and 3, cuneiform 1 remaining separate. The outer digits of the feet are usually present though small, their metapodia being reduced, and either separate or fused with the cannon bone. The placenta has few cotyledons, and there is no gall-bladder (except in *Moschus*). There are 11 genera, and about 60 species, present all over the world except in the Australian and Ethiopian regions. *Moschus* L., musk deer, without horns, upper canines large, lateral hoofs of pes well developed; musk gland on the abdomen of the male only, opening in front of the prepuce; highlands of C. and E. As. *Cervulus* de Blainv., muntjacs, hoofs but not the bones of the lateral digits present; S. and E. Asia and islands; 53 species. *Elaphodus* M. Edw., China. *Cervus* L., deer proper, 22 species, one species *C. canadensis*, the wapiti, in the Neartic region, the rest Palaearctic and Oriental; *C. elaphus* the red-deer, *C. dama* the fallow deer. *C. giganteus*, extinct Irish-elk; the genus appears in the Pliocene. *Rangifer* H. Smith (*Tarandus* Ogilby), reindeer, both sexes with antlers, arctic, circumpolar. *Alces* H. Smith, the elk or moose, arctic, circumpolar. *Cervalces* Scott, extinct, Pleistocene of N. Amer. *Capreolus* H. Smith, Eur. and C. Asia; probably 1 species, *C. caprea* the roe-deer. *Hydropotes* Swinhoe, water-deer, without antlers, with large upper canines, China. *Cariacus* Gray, N. and S. Amer., about 20 species. *Puduua* Gray, Chilian Andes, and Patagonia, 2 species.

Several extinct genera are known in Europe from the Lower Miocene onwards. In the oldest Miocene forms horns are absent, e.g. *Palaeomeryx* v. Meyer, *Amphitragulus* Pomel, and the earliest deer with horns is *Dicrocercus* Lartet from the Middle Miocene. In the later forms the horns are said to increase in complexity as the present time is approached. But this statement, like so many others of the same kind will not bear close examination, for the stag with the most elaborate antlers known (*Cervus Sedgwickii*) is from the Pliocene. All we can at present affirm is that the Miocene deer so far discovered are without horns or have only simple horns.

Fam. 12. **Giraffidae.\*** The living forms have long limbs (the anterior being the longest), long necks, and are usually provided with horns, which are covered by the ordinary skin and thus differ from the horns of all other Artiodactyls. The horns have a bony core, usually placed over the suture between the parietal and frontal bones, at first separate from the skull, but later ankylosing with it. They are present in both sexes and in the



FIG. 308.—Manus of red-deer (*Cervus elaphus*)  $\times \frac{1}{2}$ .

\* Falconer, *op. cit.*, 1868, Forsyth Major, *Proc. Zool. Soc.*, 1891, p. 315.

new-born young. In addition there is a smaller median process of the frontal, which increases with age.  $i \frac{0}{3} c \frac{0}{1} p \frac{3}{8} m \frac{3}{8}$ , molars brachyodont with rugose enamel. Lateral digits are entirely absent and the humerus has a double bicipital groove. Gall-bladder present. *Giraffa* Zimm., two living species confined to Africa; *G. camelopardalis* L., the giraffe or camelopard, lives on foliage of trees, especially the mimosa, over which its head towers to 16 feet in height, gregarious, Somaliland; *G. capensis* E. Geoff., S. Africa. The genus is found fossil in the Pliocene of Greece, Persia, and India. A second genus, *Okapia* Lankester, has recently been discovered in the Semliki forest, West Afr., it has a shorter neck, and the horns are on the frontal bone.\*

Extinct genera from the U. Miocene of S. Europe, Persia and India. *Helladotherium* Gaudry, hornless, neck shorter than in *Giraffa*, limbs nearly equal, U. Miocene of Greece and India. *Palaeotragus* Gaudry, with long horns, U. Miocene of Greece. *Samotherium* Fors. Maj., male skull with a pair of short horns, neck shorter than in *Giraffa*, U. Miocene of Samos and Persia. *Sivatherium* Falc. and Cautl., two pairs of horns, the posterior are the larger and palmated, neck short, limbs equal, Miocene of India; *Hydaspitherium* Lydekk., *Bramatherium* Falc., are similar to the last.

Fam. 13. *Antilocapridae*. The horns are on the cavicorn type, but are deciduous and branched; they contain a bony core which is not branched and not deciduous. *Antilocapra* Ord, the prong-buck, confined to N. America, 1 species.

Fam. 14. *Bovidae*.† Antelopes, sheep, goats and oxen. The horns consist of a bony core and an outer horny covering. The core is a process of the skull and frequently contains prolongations of the frontal air sinuses; the horny covering is an epidermal product; neither the core nor the horn is shed. They are present in the males of all Bovidae and in the females of many. Molars frequently hypsodont, the neck being at first hidden in the socket. The cotyledons of the placenta are numerous. Gall bladder generally present. Lateral digits usually present, represented by hoofs with or without reduced skeleton. In other respects they resemble the Cervidae. The Bovidae are the largest group of the Ungulata at the present time, containing 45 genera and about 200 species, the bulk of which are antelopes.‡ Found all over the Old World (not in Australia), five genera in the Nearctic region, absent from the Neotropical.

Sub-fam. 1. *Bubalinae*. Large African antelopes, horns in both sexes. *Bubalis* Cuv., 9 species, Afr., *B. caama* F. Cuv., the hartebeest. *Damaliscus* Sel. and Th., 7 sp., includes the bontebok and blesbok, Afr. *Connochoetes* Licht., 3 sp., includes the gnus, Afr.

Sub-fam. 2. *Cephalophinae*. Small or medium African and Indian antelopes, horns in the males only. *Cephalophus* S. Smith, with 20 sp., duikerboks, Afr. *Tetraceros* Hardw., with 1 sp., 2 pairs of horns, India.

Sub-fam. 3. *Neotraginae*. Africa, horns in male. *Oreotragus* A. Smith, with 1 sp. the klipspringer. *Ourebia* Laurillard, with 5 sp. *Raphicerus* H. Smith, with 4 sp., includes the grysbok and steinbock.

\* Lankester, *Trans. Zool. Soc.*, 16, 1902, p. 279.

† Rüttimeyer, *Rinder der Tertiären-Epoche*, *Abh. Schweiz. paläont. Ges.* 4, 1877.

‡ P. L. Sclater and O. Thomas, *The Book of Antelopes*, 1900, London.

*Nesotragus* v. Düb., with 2 sp. *Neotragus* H. Smith, with 1 sp. includes the royal antelope, only 10 inches high. *Madoqua* Og., with 6 sp.

Sub-fam. 4. **Cervicaprinae**. Waterbucks and reedbucks. Afr.; horns in male only. *Cobus* A. Sm., with 13 sp., waterbucks. *Cervicapra* Blainv., with 5 sp., reedbucks. *Pelea* Gray, with 1 sp.

Sub-fam. 5. **Antilopinae**. Horns sometimes in both sexes, Palaearctic, Oriental and Ethiopian. *Antelope* Pall., with 1 sp., black-buck, India. *Aepyceros* Sundev., with 2 sp., includes the palla, Afr. *Saiga* Gray, with 1 sp., E. Eur. and W. Asia. *Pantholops* Hodg., with 2 sp. the chiru, Tibet. *Antidorcas* Sundev., with 1 sp., the springbok, Afr. *Gazella* Blainv., with 25 sp., Palaearctic and Ethiopian. *Ammodorcas* Thom., with 1 sp., Somaliland. *Lithocranius* Kohl., with 1 sp., Afr. *Dorcatragus* Noack, with 1 sp., a pigmy form, Somaliland.

Sub-fam. 6. **Hippotraginae**. Large animals with long horns in both sexes, u. molars like those of oxen; Afr. *Hippotragus* Sundev., with 5 sp., includes the sable antelope, blaubok, equine antelope, Baker's antelope, *Oryx* Blainv., with 6 sp., Afr., extending into Arabia and Syria, horns in both sexes, includes the leucoryx, gemsbok, the beisa. *Addax* Rafin., 1 sp., N. Afr. and Arabia.

Sub-fam. 7. **Tragelaphinae**. Large bovine antelopes, Afr., with one Oriental genus, horns usually in male only. *Boselaphus* Blainv., 1 sp., the nilghai of India, female hornless. *Tragelaphus* Blainv., 6 sp., the harnessed antelopes, includes the guib, nakong, bushbuck. *Oreas* Desmar., 2 sp., includes the eland, both sexes horned, the largest antelope; and *Strepsiceros* H. Sm., the kudu.

Sub-fam. 8. **Rupicaprinae**. Intermediate between the antelopes and goats, Palaearctic and Oriental with one N. American genus. Horns in both sexes. *Rupicapra* Blainv., 1 sp., the chamois. *Nemorhaedus* H. Sm., 16 sp., Oriental, includes the goral, serow, cambingutan. *Haplocerus* H. Sm., 1 sp., the Rocky-mountain goat, California. *Budorcas* Hodg., 1 sp., the takin of Assam.

Sub-fam. 9. **Caprinae**. Sheep and goats, both sexes with horns, mainly Palaearctic, unknown before the Pliocene. *Hemitragus* Hodg., 3 sp. *Capra* L., 13 sp., goats and ibex, both sexes horned, horns flattened, males with strong odour, mountains of S. Eur., Abyssinia, Persia, Himalayas, Tibet, N. China, the Nilgherries. *Ovis* L., 22 sp., sheep, male without odour and beard, mainly Palaearctic, also Oriental and 1 sp., in N. America, essentially mountain animals. Sheep are not known before the Pleistocene. The origin of the domestic sheep is not known. *Ovibos* Blainv., 1 sp., the musk-ox, Northern part of N. Amer.

Sub-fam. 10. **Bovinae**. Cxen. Horns in both sexes, muffle naked, broad; moist; not found in S. Amer. or Madagascar; one Nearctic species. *Anoa* H. Sm., 1 sp., Celebes. *Buffelus* Rüt., 7 sp., buffaloes, India, Africa, *B. caffer* from the Cape. *Bibos* Hodgs., 4 sp., the gaur, India, the gayal, Indo-China, the banteng, Indo-China and the Islands. *Poephagus* Gray., 2 sp. *Bison* H. Sm., 2 sp., the American bison, and the aurochs (*B. bonasus*) of Europe. *Bos* L., 1 sp., now only known in the domestic state, including the varieties, *scoticus*, *primigenius* (extinct, Pleistocene), *urus*, etc. The Chillingham cattle are supposed to be but little modified descendants of *B. primigenius*. Numerous extinct genera are known from the Miocene onwards of Europe. They first appear in the Middle Miocene.

Sub-order 2. **PERISSODACTYLA**.\*

Unguligrade forms in which the axis of the limbs passes through the middle of digit No. 3, which is symmetrical in itself, and the toes of the hind foot are odd in number, never being more than three. The premolars and molars are alike, and the last lower molar is not larger than the others. The first milk molar is generally replaced. There is an alisphenoid canal and the nasals are expanded posteriorly. The number of dorso-lumbar vertebrae is always more than twenty-two. The femur has a third trochanter, the fibula does not articulate with the calcaneum, and the facets upon the distal face of the astragalus for the navicular and cuboid are very unequal and its distal surface is flattened.

These are the differential characters of the living members of the sub-order. They may need some slight qualification in dealing with the extinct members.

The dentition is frequently complete,  $i \frac{3}{3} c \frac{1}{1} p \frac{4}{4} m \frac{3}{3}$ , especially in the Eocene forms; with increased specialisation there is a tendency to the reduction of the incisors, and a loss of the upper canine and first premolar; the posterior premolars very commonly resemble the molars (except in some older forms). The grinding teeth are brachyodont in the primitive forms, and generally lophodont; but occasionally they tend to be bunodont. In the higher forms they are hypsodont, the tubercles being very long, and folded, and the valleys filled in with cement. The last lower molar is commonly without a third lobe.

The tympanic is small. The orbits are generally open behind (closed only in the *Equidae*). The dorso-lumbar vertebrae are never fewer than 22 (except in *Titanotherium*). The scapula is generally without an acromion. The ulna and fibula are complete and free in the less specialised forms, but they become slender distally and incomplete in the higher. The carpus consists of eight bones, the bones of the two rows alternate; the pollex is always absent. In the tarsus fusion of the cuneiforms may occur, otherwise the bones remain separate; there is never a trace of digits 1 and 5.

The stomach is simple, the caecum large, and the gall bladder

\* G. Cuvier, *Recherches, sur les oss. foss.*, 3rd ed., Paris, 1846. Cope, *The Perissodactyla*, *Amer. Nat.*, 1887, pp. 985, 1060. Osborn, *The evolution of the Ungulate foot*, *Trans. Amer. Phil. Soc.*, n. s., 16, 1889, p. 531.



is always absent. The cerebrum is well convoluted. The mammae are inguinal, and the testes generally descend into a scrotum or project from the inguinal canal. The placenta is diffused.

There are only three living genera; *Tapir*, *Equus* and *Rhinoceros*, but the number of extinct forms known is very great. The earliest of these are from the Eocene.

Fam. 1. **Tapiridae**.<sup>\*</sup> Short-haired forms of medium size with mobile proboscis,  $i \frac{3}{3} c \frac{1}{1} p \frac{4-3}{4-3} m \frac{3}{3}$ ; all grinding teeth brachyodont, with two transverse ridges (bilophodont);  $p$  1 of the u. jaw with a milk predecessor; posterior premolars like the molars except in the oldest fossil forms; last lower molar without a posterior lobe. Manus with 4 digits, the ulnar digit not reaching the ground, pes with 3 digits, each digit hoofed.

The orbits are not enclosed by bone, the frontals being devoid of a postorbital process; the premaxillae are small and the nasals widely separated from them; the postglenoid and paroccipital processes are large; the tympanic is reduced. Ulna and fibula well developed and separate from the radius and tibia. They are first found fossil in the Lower Eocene of Europe and N. America and endure there until the Pliocene.

*Tapirus* Cuv. Vertebrae, C 7, D 18, C 5, S 6, C 12; dentition  $i \frac{3}{3} c \frac{1}{1} p \frac{4}{3} m \frac{3}{3}$ ; the third upper incisor is larger than the upper canine but the lower canine is larger than the third incisor and bites between the third incisor and canine of the upper jaw; considerable diastema between the canines and premolar; the premolars except the first resemble the molars. There is no distinct scrotum. The two mammae are inguinal. The placentation is diffuse. They are nocturnal, inoffensive herbivorous animals frequenting forests

and the neighbourhood of water. There are 5 species, four of which are neotropical, the other being oriental in the Malay Peninsula and Sumatra. The genus is first met with in the Miocene. It is found in the Miocene and Pliocene of Europe and Asia and in the Pleistocene of America.

There is a number of extinct genera. These vary from the size of a rabbit to that of a rhinoceros. Some of them are united with the tapir and some in a sub-family the *Lophiodontinae*, which show affinities to the extinct *Palaeotheriidae*.

Extinct genera. *Lophiodon* † Cuv.  $i \frac{3}{3} c \frac{1}{1} p \frac{3}{3} m \frac{3}{3}$ ; Eocene of

<sup>\*</sup> Wortman and Earle, *Bull. Amer. Mus. N. Hist.*, 5, 1893, p. 159. Gaudry, *Bull. Soc. Géol. France* (3), 25, 1897, p. 315.

† Osborn and Wortman, *Perissodactyls of Lower Miocene Beds*, *Bull. Amer. Mus.*, 7, 1895, p. 358. Osborn, *Amer. Nat.*, 1892, p. 673.

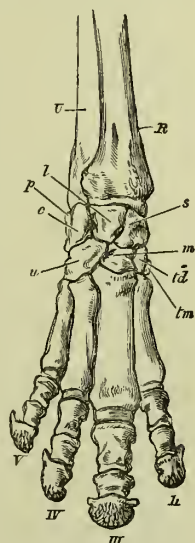


FIG. 309.—*Tapirus americanus* L. Left manus,  $\times \frac{1}{2}$ . (from Flower).



Europe, premolars simpler than molars, last lower molar with talon; *Heptodon* Cope and *Helatetes* Marse, Eocene of N. Amer.; *Colodon* Marsh, Eocene of N. Amer., Miocene of Europe. *Protapirus* Filhol, Oligocene of Europe; *Systemodon* Cope, Eocene of Amer.; *Palaeotapirus* Filhol, Eocene, Eur; *Insectolophus* Sc. and Os., Eocene of Eur. and Amer., etc.

Fam. 2. Equidae.\* Horses, asses, and zebras. Orbit closed. Grinding teeth hypsodont, with much elongated tubercles or cusps and the valleys filled in with cement;  $i \frac{3}{3} c \frac{1}{1} p \frac{4}{4} m \frac{3}{3}$ , the first premolar being small, without successor and early falling out. Upper molars with two crescentic intermediate tubercles (six cusps in all); lower with a large grooved pillar (anterior inner tubercle) at the junction of the two crescents (see p. 595). Incisors chisel-shaped, the enamel being invaginated into the crown to form the lining of a pit (the *mark*). Radius and ulna fused, the latter being very slender distally. Manus and pes three- or one-toed, the lateral digits being either complete but functionless, or reduced to their metapodia (splint bones).

Fossil remains are found in the U. Miocene, Pliocene and Pleistocene

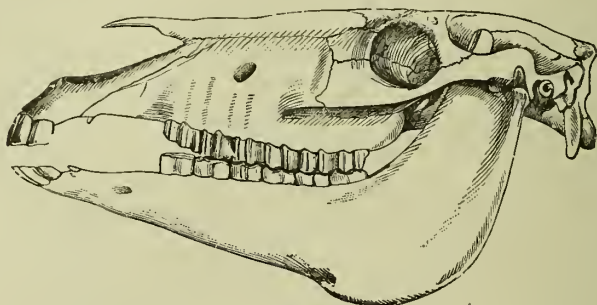


FIG. 310.—Skull of *Equus caballus*.

of Europe, Asia, N. Africa and America; at the present day represented solely by the genus *Equus* which is indigenous in Europe, Asia and Africa. *Equus* L., the only living genus. In the upper molars both inner tubercles (pillars) are connected with their respective intermediate crescentic tubercles (Fig. 312, A). Manus and pes with a single complete digit, and the proximal portions of metapodia 2 and 4 (splint bones). A callosity on the inner side of the fore-limb above the carpus. The genus first appears in the U. Miocene (? Pliocene) of India (Siwalik Hills); it is also found in the Pliocene and Pleistocene of Europe, N. Asia, N. Africa and America. Digit No. 3 alone is functional, digits 1 and 5 are entirely absent, and digits 2 and 4 represented only by the proximal ends of their metapodia (splint bones). The milk dentition is  $i \frac{3}{3} c \frac{1}{1} m \frac{4}{4}$ , the permanent

\* Marsh, *Amer. Journ. Sci.* (3), 43, 1892. Huxley, Annual Address, Geol. Soc., *Quart. J. Geol. Soc.*, 1870, 26. W. Kowalevsky, *op. cit.* Forsyth Major, Beiträge zur Geschichte der foss. Pferde, *Abh. Schweiz. pal. Ges.*, 4 and 7, 1877-86. Scott, Osteology of Meshippus, etc., *Journ. Morph.*, 3, 1891. A. Ecker, Das europäische Wildenpferd, etc., *Globus*, 34, Brunswick, 1878. J. M. M'Fadyean, *Anatomy of the Horse*, 1884. F. H. Huth, *Bibliographical Record of Hippology*, 1887.

$i \frac{3}{3} c \frac{1}{1} p \frac{1}{1} m \frac{3}{3}$ , the first premolar has no successor and falls out early (wolf tooth), and the others are similar to the molars; the last molar is not more complex than the others, nor the last milk molar than the premolar which succeeds it. The incisors are chisel-shaped and their crowns possess a deep cavity (the mark) which is formed by a fold of the enamel and eventually disappears as the tooth wears down by mastication; the first molar comes into place long before the milk-molars are shed, and the canines (tusks) are small and do not always appear in the female; there is a considerable diastema. The grinding teeth are hypsodont and grow for some time, eventually forming roots. The upper molars possess four main tubercles and two intermediate, the latter being placed between the tubercles of the anterior pair and those of the posterior pair. The two exterior tubercles are semilunar in form with their concavities outwards (Fig. 311) and are connected together, forming the doubly-concave outer wall of the tooth. The outer wall is marked by a vertical ridge formed at the concrescence of the two tubercles. The outer wall possesses therefore two concavities and is W-shaped (in the worn tooth, Fig. 312, *a*, *c*). The intermediate tubercles are also crescentic with their concavities outwards. The anterior intermediate tubercle is connected with the anterior part of the outer wall and the posterior intermediate with the middle part. These in part longitudinally and in part transversely directed crescents of the intermediate tubercles form in the worn tooth the laminae of the crown (Fig. 312, *b*<sup>1</sup>, *d*<sup>1</sup>); the spaces between them and the outer wall are filled with cement. The two inner tubercles (vertical pillar) remain tubercular, but both are connected by ridges with their respective intermediate tubercles. The anterior inner tubercle (Fig. 312, *b*) is the larger. All these tubercles are formed of enamel surrounding dentine and the valleys between them are filled up with cement which also covers the whole crown of the tooth. As a result of mastication these tubercles are worn down and islands of dentine are exposed surrounded by their enamel. In consequence of this the crown of the worn tooth is traversed by double bands of enamel containing dentine between the two laminae of each band and embedded in the cement which covers over the whole crown and fills in the valleys (Fig. 312). The enamel on the concave side of the intermediate tubercles is slightly plaited. In the lower molars there are only the four main tubercles, the intermediate tubercles being absent. The two outer tubercles are crescentic and joined to form the outer wall, but the crescents



FIG. 311.—Unworn upper molar of horse. The anterior side of the crown is to the right and the outer side is upwards (from Flower and Lydekker).

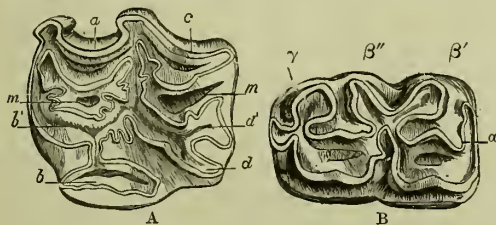


FIG. 312.—A upper, B lower molar of *Equus caballus* (from Zittel). *a* antero-external, *b* antero-internal, *b*<sup>1</sup> antero-intermediate, *c* postero-external, *d* postero-internal, *d*<sup>1</sup> postero-intermediate tubercle.  $\gamma$  posterior internal,  $\beta'$   $\beta''$  anterior internal,  $\alpha$  anterior part of anterior outer tubercle of the lower molar.

exposed surrounded by their enamel. In consequence of this the crown of the worn tooth is traversed by double bands of enamel containing dentine between the two laminae of each band and embedded in the cement which covers over the whole crown and fills in the valleys (Fig. 312). The enamel on the concave side of the intermediate tubercles is slightly plaited. In the lower molars there are only the four main tubercles, the intermediate tubercles being absent. The two outer tubercles are crescentic and joined to form the outer wall, but the crescents

are convex externally, thus differing from the corresponding tubercles of the upper molars. The outer wall, therefore, presents two convex surfaces separated by a depression (Fig. 312, *B*). The inner tubercles (vertical pillars) are grooved longitudinally on their inner faces, so that in the worn tooth the enamel bounding them presents an hourglass-shaped form. The anterior of these inner tubercles is attached to the junction of the two outer crescentic tubercles, the inner and smaller being joined to the posterior part of the posterior outer tubercle. The orbit is enclosed by bone and the aperture of the lacrymal canal is intraorbital. The tympanic is prolonged into a tubular meatus, the post-tympanic and post-glenoidal processes of the squamosal do not approach below the latter; there is a long paroccipital. Vertebrae, C 7, D 18, L 6, S 5, C 15 to 18, the centra of the cervical vertebrae are opisthocoelous. The scapula is without an acromion. The ulna and fibula are reduced and ankylosed with the radius and ulna. The carpus has seven bones, the trapezium being absent. There are two sesamoids behind the metacarpo-phalangeal articulation and one at the joint between the second and third phalanx. The femur has a third trochanter. The tarsus has six bones, the ento- and mesocuneiform being generally fused. The horse stands on the terminal phalanx of the middle digit which is covered with a horny hoof. The so-called "knee" is really the wrist, and the "hock" is the heel. The fetlock is the metacarpo-phalangeal joint, the pastern is the joint between the first and second phalanges, and the coffin-joint that between the second and third phalanges. The first phalanx is the large pastern, the second and small pastern, and the last is the coffin bone. There is a large caecum, but no gall-bladder. The interventricular septum has a cartilage and there is one precava. The cerebral hemispheres are well convoluted and the sulci are deep. There is a scrotum, and the female has a hymen, two inguinal mammae and a bicornuate uterus. The placenta is diffuse and pregnancy lasts eleven months. *E. caballus* L., the horse, the long hairs of the tail grow from the base of their organ; with a small callosity (the chestnut) on the inner side of the leg just above the hock; in Europe and Asia wild horses were formerly abundant and they have persisted in the domesticated state to the present day, but it is doubtful if there are any primitively wild horses now living; in other words the horse appears to be extinct as an originally wild animal all over the world. Horses have escaped from domestication and become feral in many parts of the world, even in America and Australia, which were without horses when they were discovered. The species is found fossil in the Pleistocene of Europe, N. Asia, N. Africa and America. *E. przewalskii* Poliakoff, C. Asia, with callosities on both limbs, but the long hairs beginning halfway down the tail. Sub-genus *Asinus*,\* asses, with the species *hemionus*, *kiang*, *onager*, *hemippus*, all from Asia, and *asinus* the domestic ass, which probably arose in Africa and was derived from the species *E. africanus* N. Africa. Sub-genus *Hippotigris* H. Smith, striped, Africa, with the species *grevyi*, *quagga* (probably now extinct), *zebra*, *burchelli*. Extinct genera *Protohippus* † Leidy (*Merychippus*, U. Miocene of N. Amer., anterior inner tubercle of the upper molars connected with its intermediate tubercle, three-toed, the outer digits not reaching the ground. *Pliohippus* Marsh, *Hippidion* Ow.,

\* Landkavel, Die wilden Einhufer Asiens., *Zool. Jahrb*, x, 1897. Prazak, *Wild Horses*, I, 1898.

† Cope, Prelim. Report Vert. Pal. Llano Estacado, *Ann. Rep. Geol. Survey Texas*, 1892, p. 20.

Pliocene of Amer. *Hipparion* \* Christol., grinding teeth less hypsodont than in *Equus* (half the length), anterior inner tubercle of upper molar isolated and laminae of enamel more plicated than in *Equus*; foot tridactyle, outer digits not reaching ground, ulna rather better developed than in the horse, about the size of a donkey; U. Miocene and Pliocene of Eur., N. Amer., and Asia.

Fam. 3. **Palaeotheriidae.** Orbits not closed, grinding teeth brachyodont, rooted, valleys not filled with cement; hinder premolars usually like the molars, rarely simpler; last lower molar with or without a third lobe; u. grinders with W-shaped outer wall; l. grinders with two crescents which at their point of union form one or two small cusps; radius and ulna separate; feet tridactyle, metapodia relatively short, the lateral digits reaching the ground; U. Eocene and Miocene of Eur. and N. Amer. *Palaeotherium* G. Cuv., u. grinders with W-shaped outer wall and two

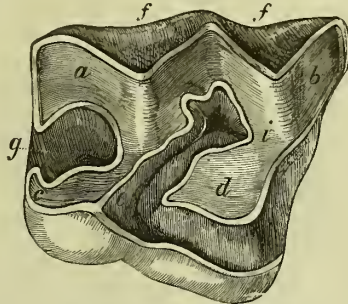


FIG. 313.—A half worn upper molar of *Palaeotherium magnum* (after Owen, from Flower and Lydekker). *ff* falciformities of outer wall, *a* postero-external tubercle (metacone), *b* antero-external tubercle (paracone), *c* postero-internal tubercle (hypocone), forming with the intermediate tubercle which is not distinct the posterior transverse ridge, *d* antero-internal tubercle (protocone) forming with the not distinct antero-intermediate tubercle *i* (protoconule) the anterior transverse ridge, *e* median valley, *g* posterior valley.

oblique transverse ridges (Fig. 313), the intermediate and inner tubercles forming the transverse ridges and not distinct from each other; in the lower molars the outer tubercles are crescentic and convex outwards (Fig. 314), but the inner tubercles (pillars of the horse) are not distinct; the three cuneiforms of the tarsus (Fig. 316, *E*) are separate; the skull is rather tapir like, and the neck shorter than in Equidae; they attain to the size of a rhinoceros; U. Eocene of Europe. *Palaeotherium* Ow., the intermediate tubercles are distinct in the u. grinders, with cement; pes (Fig. 316, *D*) as in the last, U. Eocene of Europe. *Mesohippus* † Marsh, u. grinders with W-shaped outer wall formed of the two V-shaped outer cusps, there are four other cusps not united, viz. two intermediate and two internal; a splint-like metacarpal 5, in possessing which it approximates to the next family; Oligocene of N. Amer. *Anchitherium* ‡ H. v. Meyer (Figs. 315, *C*, 316, *C*), more horse-like than the other genera of this family, incisors slightly pitted, u. grinders with W-shaped outer wall; inner tubercles connected with the outer wall by the semilunar intermediate tubercles (the distinction between the intermediate tubercles and the inner is not clear, as in

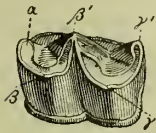


FIG. 314.—*Palaeotherium crassum*, Cuv., anterior lower molar (from Zittel). *β* antero-external tubercle, *a* antero-internal tubercle not distinct from *β*; *γ* postero-external, *γ*<sup>1</sup> postero-internal tubercle, *β*<sup>1</sup> cusp formed where the crescents meet.

\* Cope, Review of N. Amer. sp. of *Hippotherium*, *Proc. Amer. Phil. Soc.*, 1889.

† Osborn and Wortman, *Bull. Amer. Mus. N. Hist.*, 7, 1895, p. 352.

‡ W. Kowalevsky, *Mém. Akad. Imp. Sci., Petersbourg*, (7), 20, 1873.



*Palaeotherium*), with accessory tubercle behind. Odontoid process spout-like. Ulna and fibula complete, weak, fused with radius and tibia; outer digits complete but weak, U. & L. Miocene of Eur. and N. Amer. *Anchilophus* Gerv., U. Eocene, Europe. *Miohippus* Marsh, L. Miocene of

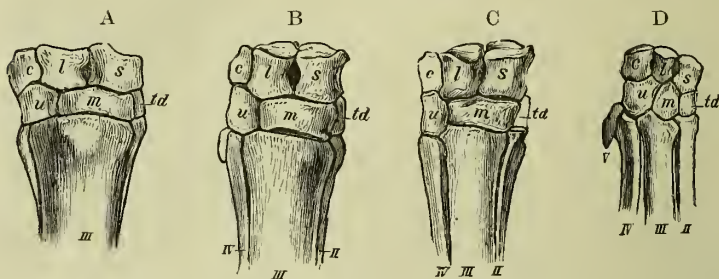


FIG. 315.—Carpus and metacarpus of A *Equus*, B *Hipparion*, C *Anchitherium*, D *Palaeotherium*. c cuneiform, l lunar, s scaphoid, u unciform, m magnum, td trapezoid, ii-v metacarpals (from Zittel).

Amer.; [*Desmathippus* Scott, U. Miocene, Amer., with brachyodont grinders, valleys with thin cement, very similar to preceding, but if anything nearer to *Protohippus* in its digits. In this series of genera *Anchitherium* is perhaps the most equine, but its grinders depart

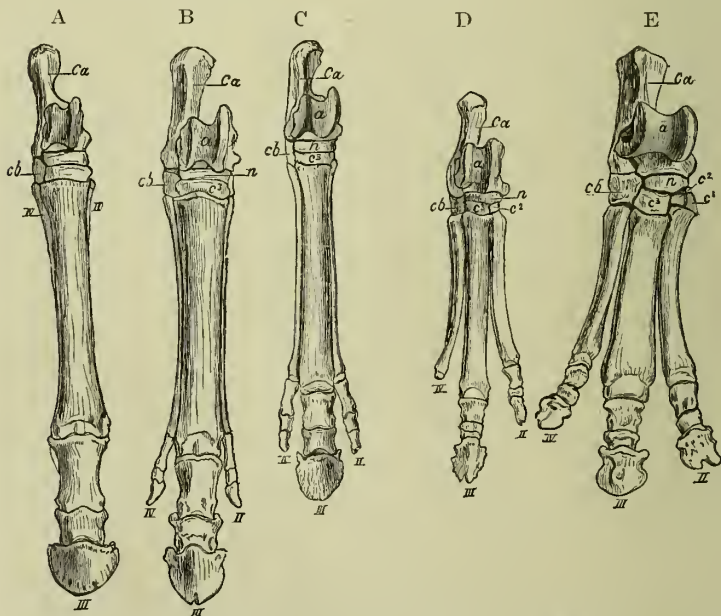


FIG. 316.—Right pes of A *Equus*, B *Hipparion*, C *Anchitherium*, D *Palaeotherium*, E *Palaeotherium*. ca calcaneum, a astragalus, n navicular, cb cutoid, c1-3 three cuneiforms, ii-iv second to fourth toes (from Zittel).



considerably from the equine type of pattern and resemble those of *Palaeotherium* which is the most tapir-like.

Fam. 4. **Hyracotheriidae**.<sup>\*</sup>  $i \frac{3}{3}$   $c \frac{1}{1}$   $p \frac{4}{4}$   $m \frac{3}{3}$ ; grinders low and tubercular, premolars (usually tritubercular) simpler than the molars; upper molars (Fig. 317, A) with six cusps, lower (Fig. 317, B) with four; tubercles conical or V-shaped, ridges low; orbit not closed, but post-orbital process of frontal present; odontoid conical; radius and ulna subequal, separate; scapula with a well-marked coracoid process; manus with four (without trace of No. 1), pes with three digits. They are the oldest Perissodactyls and are confined to the Eocene of Eur. and N. Amer. Their grinders are practically bunodont, at any rate in the upper jaw where there are hardly any outer wall or ridges. *Hyracotherium* Ow., a smallish animal, about 3 feet long, Lower Eocene of Eur., and N. Amer.; *Eohippus* Marsh, and *Protorohippus* Wort., Eocene, N. Amer.; *Orohippus* (*Epihippus*) Marsh, and *Pachynolophus* Pomel, Eocene of Eur. and Amer. teeth more equine with ridges connecting the tubercles; *Propalaeotherium* Gerv., M. Eocene, Eur., etc.

Much has been written on the ancestry of the horse. It has been maintained by many authors that a continuous series of forms connecting it with the four-toed, brachyodont, bunodont Hyracotheriidae of the Eocene has been discovered and that here if anywhere a demonstrative historical proof has been obtained of the truth of the doctrine of organic evolution. Without desiring in the smallest degree to impugn that doctrine, it may be permitted us here to examine rather closely the view that the series of forms which recent palaeontological research has undoubtedly brought to light constitute that historical proof which has been claimed for them.

The forms which are utilised for this series are: *Pliohippus*, *Protohippus*, *Desmathippus*, *Miohippus*, *Mesohippus*, *Orohippus* and *Hyracotherium*. The characters which are chiefly pointed to as showing the gradation are those of the limbs, and the teeth, and to a certain extent of the skull. Beginning at the lower end of the series, we find in *Hyracotheriidae*, brachyodont molars which are practically bunodont, a complete dentition, premolars simpler than the molars, a well marked coracoid process on the scapula, a conical odontoid process, an orbit not closed in by bone though the frontal has a postorbital process, four complete digits on the manus and three on the pes, radius and ulna nearly equal in size and separate. In the stage next succeeding in the ascending order—*Palaeotheriidae*—we find these characters modified as follows: the teeth are still brachyodont with little cement, low ridges connect the tubercles, the hinder premolars are usually like the molars, a complete dentition; the orbit is still open; the radius and ulna are still separate and about equally developed, but the manus is tridactyle, digit No. 5 having become reduced

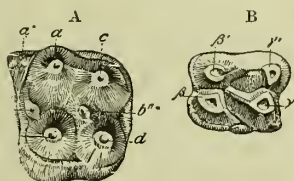


FIG. 317.—*Hyracotherium leporinum* Ow. A second upper, B first lower molar. The tubercles are: *a* antero-external, *a'* accessory, *b* postero-external, *b'* antero-intermediate, *b''* postero-intermediate, *c* postero-external, *d* postero-internal;  $\beta$  antero-external,  $\beta'$  antero-internal,  $\gamma$  postero-external,  $\gamma'$  postero-internal (from Zittel, after Owen).

<sup>\*</sup> Wortman, Species of *Hyracotherium*, etc., *Bull. Amer. Mus. Nat. Hist.*, 8, 1896, p. 81. Earle, Comparison of the American and European forms *Hyracotherium*, *Amer. Nat.* 1896, p. 131.

to the merest vestige of its metacarpal, the pes is very similar to that of the preceding family. The changes here, as compared with the previous family, are the presence of ridges connecting the tooth-cusps, the reduction of digit No. 5 of the manus.

We now come to the Equidae, where we find *Protohippus* with hypsodont molars, about half the length of those of *Equus*, and valleys filled in with cement, the anterior inner tubercle of the upper molars is connected with the intermediate tubercle, orbit closed, manus and pes tridactyle, the outer digits not reaching the ground, no trace of any other digits, ulna slender distally and fused with radius. Lastly we have *Pliohippus* with rather longer grinders, very similar to *Equus* in pattern, without lateral digits, the metacarpals only being represented; ulna and fibula still more approximating to the condition found in *Equus*.

So far as the characters mentioned are concerned, we have here a very remarkable series of forms which at first sight appear to constitute a linear series with no cross-connections. Whether, however, they really do this is a difficult point to decide. There are flaws in the chain of evidence, which require careful and detailed consideration. For instance, the genus *Equus* appears in the Upper Siwalik beds, which have been ascribed to the Miocene age. It has, however, been maintained that these beds are really Lower Pliocene or even Upper Pliocene. It is clear that the decision of this question is of the utmost importance. If *Equus* really existed in the Upper Miocene, it was antecedent to some of its supposed ancestors. Again in the series of equine forms, *Mesohippus*, *Miohippus*, *Desmathippus*, *Protohippus*, which are generally regarded as coming into the direct line of equine descent, Scott \* points out that each genus is, in some respect or other, less modernised than its predecessor. In other words it would appear that in this succession of North American forms the earlier genera show, in some points, closer resemblances to the modern *Equus* than to their immediate successors. It is possible that these difficulties and others of the same kind will be overcome with the growth of knowledge, but it is necessary to take note of them, for in the search after truth nothing is gained by ignoring such apparent discrepancies between theory and fact.

Fam. 5. **Rhinocerotidae.**† Large unwieldy pachyderms, usually with one or two epidermal horns on the strongly arched nasal and frontal bones;  $i \frac{3 \text{ to } 0}{3 \text{ to } 0}$   $c \frac{1 \text{ to } 0}{1 \text{ to } 0}$   $p \frac{4 \text{ to } 2}{4 \text{ to } 2}$   $m \frac{3}{3}$ , complete only in the oldest types; incisors and canines frequently absent; premolars like the molars but simpler in the older forms; last lower molar without third lobe; u. grinders, with thick outer wall, nearly flat with obliquely transverse laminae, lower grinders with two semilunar ridges joining to form the outer wall. The orbit is widely open behind and the frontal is without a postorbital process; the nasals are extensive; the postglenoid processes very large and may or may not unite with the post-tympanic process of the squamosal to form a false external auditory meatus; the tympanic is annular. Ulna and radius, tibia and fibula complete. Manus with 3 or 4, pes with 3 digits; digit No. 3 is larger than the others and symmetrical in itself, digit No. 1 is not present, and digit No. 5 when present in the manus is smaller than

\* *Trans. American Philosophical Society (N.S.)* 18, 1896, pp. 119, 120.

† Lydekker, Notes on Rhinoceroses ancient and modern, *Field*, 79, p. 903, and 80, p. 38, 1892. Pavlow, Les Rhinocerotidae de la Russie, etc., *Bull. Nat. Moscou*, 1892, p. 147.

the others ; it is never present in the pes. They have short necks and legs and a very thick skin with scanty hair, and often folded so as to give them the appearance of being armoured. The horns are purely epidermal structures without bony core ; they have been compared to a mass of agglutinated hairs. The anterior horn is on the nasal bones, the posterior, which is absent when there is only one, on the frontals. The stomach is simple, the villi of the small intestine long, there is no gall bladder. The testes hardly project, the uterus is bicornuate and the two mammae inguinal.

They are stupid timid animals, but ferocious when attacked. They often inhabit swampy regions and like wallowing in water or mud. At the present day they are found in Africa, the Malay Islands, and tropical India. They are known fossil from the U. Eocene onwards in the Old and New Worlds, but they become extinct in America at the end of the Pliocene. There is but one living genus, *Rhinoceros* L. (including the genera *Ceratohinus* Gray and *Atelodus* Pom.), the incisors are variable and often fall out early, there are no upper canines, the peculiar cutting teeth of the front of the lower jaw are probably canines,  $p \frac{1}{4} m \frac{3}{3}$  ; the first milk molar is smaller than the others and not always replaced ; the grinders form roots early and the valleys are not filled in with cement. Vertebrae C 7, D 19-20, L 3, S 4, C about 22. Manus and pes with three hoofed digits ; in the manus there is a rudiment only of metacarpal 5.

The living species are *R. unicornis* L., India, with one horn ; *R. sondaicus* Desm., with one horn, Java, India, etc. ; *R. sumatrensis* Cuv., Malacca, Sumatra, Borneo, two horns ; *R. sinus* Burchell, the white rhinoceros, Africa, two horns ; *R. bicornis* L., Africa, two horns. Many extinct species from the Miocene of the Old World onwards. It is therefore like the tapir a very ancient type. *R. antiquitatis* Blumenb. (*tichorhinus* Cuv.) is the woolly rhinoceros of the Pleistocene of Europe—a huge animal with two horns, the carcasses of which with those of the mammoth have been discovered in N. Siberia.

A large number of fossil genera, which have been arranged in sub-families, are known from the earlier tertiary strata of the Old and New Worlds from the U. Eocene onwards. Many of the older of these forms are characterised by having a complete dentition, premolars simpler than the molars, and a fully developed, though slender digit No. 5 on the manus. It is impossible to deal with these here, but one or two may be mentioned. *Hyrachinus* Leidy, U. Eocene of N. Amer. with 4 toes on manus. *Hyraodon* Leidy, with 3 toes in manus, L. Miocene of N. Amer., both with complete dentition, without horns and with longer limbs and neck, and in their general build more resembling *Architherium* than modern rhinoceroses. *Aceratherium* Kaup., hornless, with  $i \frac{1}{4} c \frac{0}{0} p \frac{1}{4} m \frac{3}{3}$ , and 4 toes on the manus, from the U. Eocene of France and Pliocene of India ; *Diceratherium* Marsh, with two horns, U. Miocene, N. Amer. *Elasmotherium* Fisch., Pleistocene of Siberia, a huge beast with 2 horns, with  $p \frac{2}{2} m \frac{3}{3}$ , enamel much plicated, very hypsodont and valleys filled with cement ; *Amynodon* Marsh, is the type of an ancient and primitive group from the U. Eocene of N. Amer.

Here may be placed provisionally the **Titanotheriidae**,\* which depart in

\* Earle, A memoir upon the genus *Palaeosyops* Leidy and its allies, *Journ. Acad. Philadelphia*, 9, 1892, p. 267. Osborn, Revision of the genus *Telmatotherium*, *Bull. Amer. Mus. N. Hist.*, 7, 1895, p. 82, and 346.

some important respects from the perissodactyl type, e.g. the fore-foot is artiodactyl-like, and the number of dorso-lumbar vertebrae is less than 22. They are huge extinct beasts from the Eocene and Miocene of N. America and probably of Europe. They possessed two bony horn-like prominences on the nasal bones.  $c \begin{smallmatrix} 3 \text{ to } 0 \\ 3 \text{ to } 0 \end{smallmatrix} i \begin{smallmatrix} 1 \\ 1 \end{smallmatrix} p \begin{smallmatrix} 4 \\ 4 \text{ to } 3 \end{smallmatrix} m \begin{smallmatrix} 3 \\ 3 \end{smallmatrix}$ ; grinding teeth brachyodont with a W-shaped outer wall and two inner tubercles with low connecting ridges. Manus with 4 digits, artiodactyl-like, axis passing between digits 3 and 4, pes perissodactyl with 3 digits. The bones of the two carpal rows alternate. Premolars like the molars in the later forms, simpler in the older; femur with a small third trochanter, and the fibula articulates with the calcaneum. The orbits were open behind. The brain cavity was small and there was a small, much convoluted cerebrum. There appear to have been only 19 or 20 dorso-lumbar vertebrae, a character which also recalls the artiodactyls; probably omnivorous. *Lambdotherium* Cope, *Palaeosyops* Leidy, *Titanotherium* Leidy, *Brontotherium* and *Brontops* Marsh.

### Sub-order 3. LIPOTERNA.\*

They are remarkable extinct American digitigrade ungulates,† which in the structure and reduction of their digits (the axis of the limb passing through the third digit) and in the structure of their lophodont grinding teeth resemble the Perissodactyla; but they differ from them in the carpal and tarsal bones not alternating, and in the fact that the fibula articulates with the calcaneum as in Artiodactyls. The humerus is without an entepicondylar foramen. The digits vary in number from five to one. The astragalus is flattened below, the carpus has no centrale, the orbit is usually closed, there is a third trochanter on the femur, and there is no clavicle. The brain case is small and the dentition complete or slightly reduced. The group is not well known, but the digits and the teeth show variations not unlike those presented by the same organs in the Perissodactyls. For instance the digits vary from five to one, the teeth show a tendency to reduction in some genera, but these variations do not form a continuous series as in the Perissodactyls. The oldest forms, e.g. *Thoatherium* from the Eocene of Patagonia show a reduction in the teeth and of the digits to the equine condition, and a diastema between the incisors and grinders, whereas in the comparatively recent form *Macrauchenia* from the Pliocene, the dentition is complete, the feet have three digits, and there is no gap in the tooth series. A remarkable feature of the Macrauchenidae is the presence of a mark in the incisors as in the Equidae, and in the same family the vertebral canal pierces the neural arches of the cervical vertebrae as in the camels and *My. mecophaga*. It can hardly be supposed that the sub-order is related to the Perissodactyls, but the resemblances are certainly remarkable.

Fam. 1. **Macrauchenidae.** Dentition  $i \begin{smallmatrix} 3 \\ 3 \end{smallmatrix} c \begin{smallmatrix} 1 \\ 1 \end{smallmatrix} p \begin{smallmatrix} 4 \\ 4 \end{smallmatrix} m \begin{smallmatrix} 3 \\ 3 \end{smallmatrix}$  in a closed row; incisors with a "mark," anterior premolars simpler than the molars, grinders rhinocerotine; nasal openings far back, nasal bones reduced or aborted;

\* Ameghino. Contrib. al conocim de los Mamíferos foss. d. l. Republ. Argent., *Actas Ac. nac. Cordoba*, 1889, 6, p. 523, and *Revista Argentina*, 1, 1891. Cope, The Lipoteria, *Amer. Nat.*, 25, 1881. Gervais, *Mém. Soc. Geol. France*, (2), 9, 1873.

† The reasons for placing this sub-order among the ungulates are stated on p. 574.



feet 3- or 5-toed ; vertebrarterial canal perforating neural arches of cervical vertebrae. Tertiaries of S. America. *Theosodon* Am., orbit open behind, manus and pes with 5 digits, the outer being much reduced ; Eocene, Patagonia. *Macrauchenia* Ow., manus and pes with three digits, orbit closed ; femur with third trochanter ; Miocene and Pliocene S. Amer.

Fam. 2. **Proterotheriidae.** Nasal bones elongated, orbit closed, dentition  $i \frac{1}{2} c \frac{0}{0} p \frac{4}{4} m \frac{3}{3}$ , with short diastema, grinders resembling those of *Anchitherium*. Limbs 3- to 1-toed, the lateral metapodia weak. Tertiaries of S. America. *Proterotherium* Amegh., Eocene, Miocene, S. Amer., with 3 toes. *Thoatherium* Am., with one toe, Eocene, Patagonia.

### Order 9. AMBLYPODA.\*

*Extinct semiplantigrade animals with pentadactyle hoofed limbs, interlocking carpals and tarsals, and very small brain. There is no clavicle. A centrale is sometimes present in the carpus and an entepicondylar foramen in the humerus. The grinders are lophodont, and usually brachyodont.*

We separate this order very doubtfully from the Ungulata. It presents most of the ungulate features, and the grinders are ungulate-like. The most remarkable character of the group is the minute size of the brain which seems to separate it from all other mammals (Fig. 319, A).

They are extinct, usually large, semiplantigrade animals with short, hoofed, pentadactyle feet and broad terminal phalanges (Fig. 319). The dentition is usually complete, and the grinders are brachyodont and lophodont. The brain is very small and smooth, smaller and simpler than in any other known mammal. The orbit is open behind. The ulna and fibula are free and well developed. The carpalia alternate slightly and a centrale is sometimes present, the astragalus is flattened and articulates largely with the cuboid and with the tibia and fibula, and the femur has a third trochanter only in the earlier forms. There appears to be no clavicle, but the scapula has a large acromion. There is an entepicondylar foramen in *Pantolambda*, but not in the more recent forms. The *Amblypoda* present a certain resemblance to the elephants in their size, feet and the general structure of their limbs ; but the resemblance is only superficial. The head and dentition of the two groups differ totally, and the resemblance in the limbs is quite superficial. For instance there is no interlocking of the carpal and tarsal bones in the elephant, and the astragalus is quite different in shape in the two groups. Moreover the elephant has no third trochanter. They are found in Europe and America and are confined to the Eocene. The earliest forms are from the Lower Eocene. *Pantolambda* Cope, L. Eocene, New Mexico, of moderate size, dentition complete, grinders tritubercular, skull without horns, femur with third

\* Cope, The Amblypoda, *Amer. Nat.*, 1884 and 5. Earle, Revision of the species of Coryphodon, *Bull. Amer. Mus. N. Hist.*, 4, 1892. Marsh, Monograph of the Dinocerata, *U. S. Geol. Surv.*, 10, 1884. Osborn, *Bull. Amer. Mus. N. Hist.*, 16, 1898.



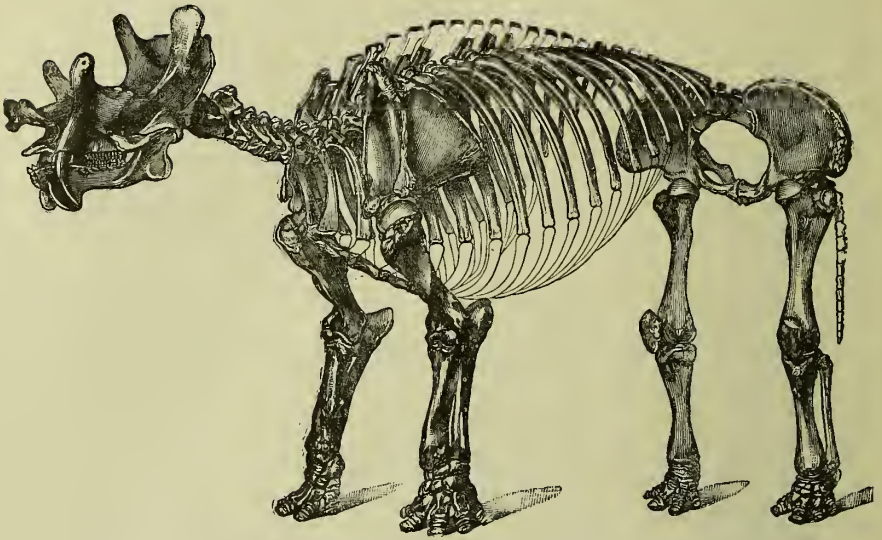


FIG. 318.—*Tinoceras ingens*, skeleton  $\times \frac{1}{30}$ , restored (after Marsh, from Woodward).

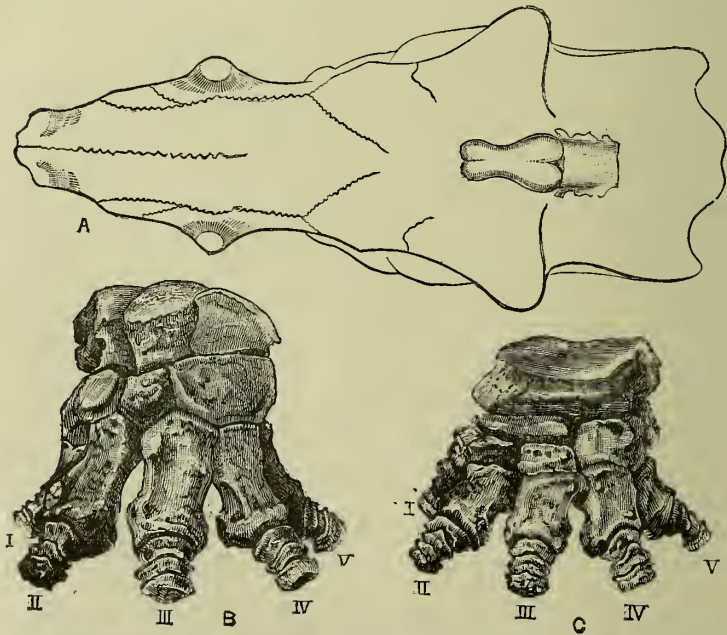


FIG. 319.—*Dinoceras mirabile*. A outline of dorsal aspect of skull, showing size and form of brain cavity,  $\times \frac{1}{4}$ . B left manus, and C left pes,  $\times \frac{1}{2}$  (after Marsh, from Woodward).

trochanter; scapular and neural spines as in the next, carpus with centrale, humerus with entepicondylar foramen. *Coryphodon* Ow., dentition complete, canines large, grinders ridged, neural spines weak, skull smooth, without horns; scapula characteristic, narrow above, shaped like a leaf; tibia articulates with the calcaneum and astragalus; femur with third trochanter; about the size of a tapir, probably omnivorous; this genus was first made known by a fragment of a jaw dredged in the sea off the coast of Essex. Lower Eocene of Europe and America. *Dinoceras* Marsh (*Uintatherium* Leidy), approaching the elephants in size, with three pairs of bony horn-like prominences on the skull, formed by prolongations of the parietals, maxillaries, and nasals. Dentition  $i \frac{9}{3} c \frac{1}{1} p \frac{3}{3 \text{ to } 4} m \frac{3}{3}$ , canines as large tusks; neural spines short; scapula broad above; limbs elephantine, carpus without centrale (Fig. 319, B) and femur without third trochanter, fibula articulating with the astragalus only; M. and U. Eocene, N. Amer. *Tinoceras* Marsh (*Loxolophodon*), contains the largest forms (Fig. 318). The genus *Arsinoitherium* Beadnell\* from the Upper Eocene of the Fayum of Egypt may be placed provisionally in this order. It was a large animal with a massive skull bearing two pairs of horns, the larger of which were furnished by the great nasal bone, and the smaller by the frontals. The squamosal is large and there are large post-tympanic and postglenoid processes, which approach one another below the auditory meatus. The dentition is  $i \frac{3}{3} c \frac{1}{1} p \frac{1}{4} m \frac{3}{3}$ , the tooth series is closed, and there is no clear distinction between the incisors, canines, and premolars. The premolars and molars are hypsodont and lophodont and easily distinguishable. The scapula resembles that of *Dinoceras*, as do the tibia and tarsus. The femur is without a distinct third trochanter.

### Order 10. TOXODONTIA. †

*Extinct semiplantigrade or plantigrade animals with tridactyle limbs, hypsodont, rodent-like grinders, without clavicles and entepicondylar foramen in the humerus. There is a centrale in the carpus. The carpal bones interlock but the tarsals are serial.*

They are all extinct, South American forms and were herbivorous and plantigrade. The dentition is usually complete, but the canines tend to be weak or aborted. The grinders are prismatic and somewhat rodent-like, resembling those of the Typotheria. The fibula articulates with the calcaneum.

\* Beadnell, A preliminary note on *Arsinoitherium zitteli*, Beadn., from the Upper Eocene strata of Egypt, *Survey Department Public Works Ministry*, Cairo, 1902. Andrews, *Geological Mag.*, n. s., 5, 1, p. 109 and 157.

† Burmeister, *Ann. Mus. Buenos Ayres*, 1, 1867, and 3, 1869. Cope, On *Toxodon*, *Proc. Amer. Phil. Soc.*, 1881. Owen, *Toxodon* in the Zoology of the *Voyage of the Beagle*, 1840, and *Nesodon*, *Phil. Trans.*, 1853. Lydekker, *op. cit.*, under Typotheria. Roth, *Revista Mus. La Plata*, 6, 1895, p. 333.

The earliest forms are from the Cretaceous of Patagonia, but the bulk are from the Eocene. They extend through the Miocene into the Pliocene where the first of them, *Toxodon*, was found by Darwin in the Pampas Formation.

The dentition though often complete and continuous is very highly specialised. The grinders are peculiar and can hardly be said to be ungulate-like. The skull is massive, and high behind; the nasals project freely and are sometimes short and suggest a proboscis; the lacrymals are small and the orbits open behind. It is difficult to say what affinities the skull suggests. The structure of the fore-limbs in the form of the scapula, the absence of a clavicle and the tridactyle manus, recalls the rhinoceros. The same may be said of the hind limb, but the third trochanter is small or absent, and the tarsalia are successional. These points militate against perissodactyl affinities, as does the presence of a centrale in the carpus. On the whole it is difficult to see why these animals should have been placed with the Ungulata, unless it be because they cannot be related to any other group.

*Nesodon* Ow., of small or moderate size, with nasal opening directed forwards; cerebrum large and much convoluted;  $i \frac{2}{3}$   $c \frac{1}{4}$   $p \frac{1}{4}$   $m \frac{2}{3}$  in almost continuous series and most of the teeth rooted; femur with small third trochanter, and feet tridactyle and digitigrade; Eocene, Santa Cruz Formation. *Toxodon* Ow., large animals with nasal openings further back, dentition reduced  $i \frac{2}{3}$   $c \frac{0-1}{1}$   $p \frac{4}{3-4}$   $m \frac{2}{3}$ , all rootless, scapula without acromion, radius crossing the ulna as in Proboscidea, carpalia alternating, femur without third trochanter, extremities tridactyle and plantigrade, Miocene, Pliocene.

### Order 11. TYPOTHERIA.\*

*Extinct pentadactyle plantigrade animals, with a clavicle, an entepicondylar foramen in the humerus, serial or interlocking carpus, and an opposable hallux. A centrale is present in the older forms, and the grinders are rodent-like.*

If it was difficult to settle the position of *Hyrax* in the mammalian series, it must be still more difficult to settle that of the present group for all its members are extinct and there is no living form to assist us with its soft parts. They are generally placed with the Ungulata, though it is difficult to see their ungulate affinities. They show some resemblances to *Hyrax*, and to rodents.

Hitherto the Typotheria have only been found in South America. They are first met with in the Cretaceous, but the

\* Ameghino, *Contrib. al Conoc. de los Mamíferos de la Republ. Argentina*, Buenos Aires, 1889, and *Revista Argentina de Hist. Nat.*, 1, 1891. Gervais, *Remarques sur le Typotherium*, *Zool. et Paléont. générales*, 1. Lydekker, A study of extinct Argentine ungulates, *Ann. Mus. La Plata, Palaeont. Argentina*, 2, 1893, 1894.

bulk of them are found in the Eocene, though they extend through the Miocene into the Pliocene.

Their general characters may be described as follows. They were small animals, about the size of *Hyrax*. The brain cavity is small and the brain was smooth; the orbit is not closed though the frontal has a well marked postorbital process. The skull on the whole recalls that of *Hyrax*, and in certain features that of rodents and of the Toxodontians. The dentition is in the oldest forms complete and almost in a closed series. It is in many respects like that of the Toxodontia. The grinders are hypsodont and rodent like. In the older forms the teeth seem to have been rooted, but in the more recent they were rootless. The scapula has a coracoid process and its spine has an acromion and a peculiar backwardly directed process as in elephants and some rodents, and there is a clavicle. The humerus has an entepicondylar foramen. The ulna and radius are separate and capable of rotation. The fibula articulates with the calcaneum and is separate from the tibia. The femur has a third trochanter. The carpus has a centrale in the older forms, and the arrangement of the two rows of bones is successional in the other, alternating in the more recent forms. The manus possesses five digits, and the distal phalanges are either broadened and hoof-like or split, like that of digit No. 2 of the foot of *Hyrax*. The pollex appears in some cases at any rate to have been opposable. In the foot the distal phalanges are broadened and the hallux was opposable. The sacrum was composed of seven vertebrae as in some edentates. *Protypotherium* Am.,  $i \frac{3}{4} c \frac{1}{4} p \frac{4}{4} m \frac{3}{4}$  in a nearly closed series: carpalia serial, with centrale, the pes has 5 digits, the fibula articulate with the calcaneum, Eocene and Miocene. *Icochilus* Am., Eocene. *Typotherium* Bravard,  $i \frac{1}{2} c \frac{0}{4} p \frac{2}{4} m \frac{3}{4}$ , with wide diastema, grinders rootless; carpalia alternating, without centrale; fibula articulating with astragalus; pes tetradactyle; attains the size of a pig; Miocene, Pliocene.

### Order 12. TILLODONTIA.\*

This is a group of extinct forms from the Lower and Middle Eocene of N. America and according to Ameghino from the Cretaceous of Patagonia, and there are fragmentary remains (*Platychaerops* Charlesw.) from the Eocene of England. The group is not well known but the characters, so far as ascertained, are as follows. Plantigrade, pentadactyle, with clawed digits; and rodent-like incisors growing from continuous or long-persistent pulps, and with enamel only on their anterior face; the u. grinders are tritubercular, the lower tubercular-sectorial. The premaxillae are large; there is no postorbital process on the frontal; the humerus has an entepicondylar foramen, and the femur a third trochanter. The skeleton presents resemblances to the Carnivora. The dentition when complete is  $i \frac{3}{4} c \frac{1}{4} p \frac{3}{4} m \frac{3}{4}$ , but the first and third incisors are smaller than the second large rodent-like pair and may be absent. The canines also tend to be reduced. The brain was small and weakly furrowed. The Tillodontia were large and medium-sized land animals with likenesses to the Carnivora and Rodentia and are often associated with the latter in classification,

\* Marsh, *Tillotherium*, *Amer. Journ. Sci.* (3), 9, 1875, p. 221, and 11, 1876, p. 249. Cope, *Vertebrata of the Tertiary Form. of the West*, 1877. Wortman, *Ganodonta*, *Bull. Amer. Mus. N. Hist.*, 9, 1897, p. 59.



*Esthonyx* Cope, Lower and Middle Eocene (Wasatch and Bridger), *Anchipodus* Leidy, Bridger Eocene; *Tillotherium* Marsh, Bridger Eocene, the most specialised with dentition  $i \frac{2}{2}$   $c \frac{1}{1}$   $p \frac{3}{2}$   $m \frac{3}{3}$ , incisors very rodent-like, but lower jaw with transverse condyle.

Here may be mentioned the *Taeniodonta* Cope (*Stylinodonta* Marsh) lately renamed *Ganodonta*,\* known by fragmentary remains. The dental series is continuous or nearly so; there is a tendency to reduction of incisors, and the canines are large and sometimes resemble rodent incisors; the grinders are bilophodont or quadrituberculate (or tritubercular) and

there appears to be a deficiency of enamel; in some species there is hypsodonty and growth from persistent pulps; the radius and ulna appear to have admitted of pronation and supination of the manus, a clavicle is present, and the digits had curved claws; there was a weak third trochanter. A fragmentary manus seems to resemble that of a ground-sloth, and on this evidence together with the poverty of enamel in the molars and certain features of the pelvis and vertebrae has been evolved the certainty that these animals are the Eocene fore-

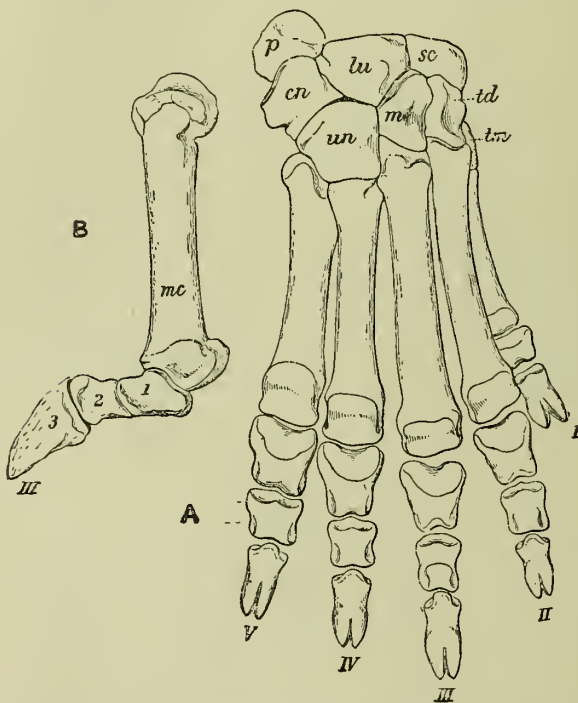


FIG. 320.—*Homalodontotherium segoviae*, A right manus, B third digit in side view,  $\times \frac{2}{3}$  (after Ameghino, from Woodward). *cn* cuneiform, *lu* lunar, *m* magnum, *mc* metacarpal, *p* pisiform, *sc* scaphoid, *td* trapezoid, *tm* trapezium, *un* unciform, *i-v* digits, 1-3 phalanges.

runners of the Edentata. All are from the Lower Eocene (Puerco, Wasatch and Bridger Beds) of N. America. *Hemiganus* Cope, Puerco Beds. *Psittacotherium* Cope, Upper Puerco, this is the genus of which the ground sloth-like manus is known, canines and grinders rooted. *Calamodon* Cope, Wasatch Beds, and Eocene of England, with large rootless canines like a rodent incisor, grinders with roots. *Stylinodon* Marsh, Wind River, and Bridger Eocene, canines and all lower teeth rootless. It is quite possible that the *Ganodonta* are allied to the Edentata, but there

\* Wortman, *op. cit.*

is a large step from the admission of that possibility to the definite assertion that they are the ancestors of that order.

The **Conoryctidae** with *Conoryctes* and *Onychodectes* Cope, from the Puerco Eocene, are possibly allied here.

### Order 13. **ANCYLOPODA.\***

Plantigrade forms with 3 or 5 digits apparently ending in claws. They appear to have possessed characters common to a number of groups. When first discovered they were placed with the Edentata, but their grinders are perissodactyl-like. On the other hand they may be without a third trochanter on the femur and the axis of the limb does not pass through the third digit. The bones of the two carpal rows alternate, but the tarsals are serial. They are found in the Cretaceous and Eocene of Patagonia, in the Eocene of Europe, the Miocene of Europe, America and Asia and a few in the Pliocene. *Homalodontoherium* Huxley, pentadactyle (Fig. 320), complete dentition, Eocene, Patagonia; *Chalicotherium* Kaup., tridactyle, without incisors, Miocene, Europe; *Macrotherium* Lartet, Miocene, Europe.

### Order 14. **CONDYLARTHRA.†**

*Extinct, plantigrade or digitigrade animals with pentadactyle limbs, without hoofs; without a clavicle. Carpalia and tarsalia sometimes serial, sometimes interlocking. The carpus usually with a centrale. Dentition complete; grinding teeth brachyodont and bunodont. The humerus has an entepicondylar foramen and the femur a third trochanter. From the Eocene of America, and a few remains in the Eocene of Europe.*

They had a very small brain with an uncovered cerebellum and a smooth cerebrum. The skull is elongated with orbits widely open behind, the frontals and jugals being devoid of postorbital processes. The canine teeth are not much enlarged and the premolars are simpler than the tritubercular or quadritubercular molars. There is no clavicle. The humerus has an entepicondylar foramen, therein differing from that of Ungulata. They are commonly described as

\* Ameghino, *Enum. Synopt. des Mammif. tert. de Patagonie*, 1894. Flower, *Homalodontoherium*, *Phil. Trans.*, 1874. Huxley, *Quart. J. Geol. Soc.*, 1870. Filhol, *Études sur les Mammif. de Sansan*, *Ann. Sci. géol.*, 1891, 21. Osborn, *Amer. Nat.* 22, 25, 26, 27, 1889-93. Cope, *Amer. Nat.*, 1889, p. 658.

† Cope, *Synopsis of the Vert. Fauna of the Puerco Series*, *Amer. Phil. Soc.*, 16, 1888. Osborn and Earle, *Fossil Mam. of the Puerco Beds.*, *Bull. Amer. Mus. N. Hist.*, 7, 1895. Matthew, *A Revision of the Puerco Fauna*, *ibid.*, 9, 1897, p. 259. Osborn, *Phenacodus*, *ibid.*, 10, 1898. Marsh, *Hyracops*, *Amer. Journ. Sci.* (3), 43 1892.

plantigrade, but *Phenacodus* was digitigrade. The carpus and tarsus (Fig. 321) are very similar to those of *Procyon* (Fig. 290); the bones of the two rows are usually serially arranged and the navicular articulates laterally with the cuboid. The astragalus has a neck and convex distal surface, and resem-

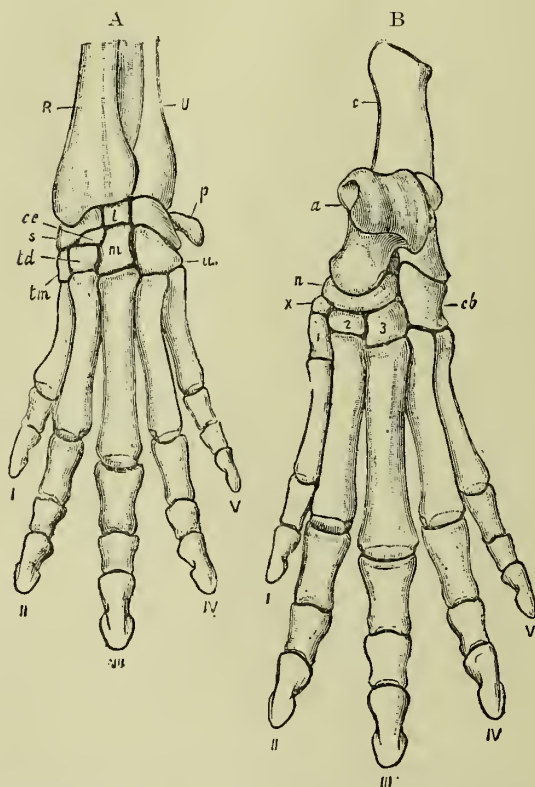


FIG. 321—*Hyracops socialis* Marsh. Lower Eocene, Wasatch. A left manus, B left pes (after Marsh, from Woodward). R radius, U ulna, s scaphoid, l lunar, p pisiform, ce centrale, tm trapezium, td trapezoid, m magnum, u unciform, ca calcaneum, a astragalus, n navicular, cb cuboid, 1, 2, 3 cuneiforms, x epicuneiform.

bles that of the Creodonta. The three middle digits are longer than the outer, and the axis of the limb traverses digit No. 3 as in Perissodactyla. The terminal phalanges are expanded and pointed and must have carried hoof-like nails. The femur has a third trochanter — another perissodactyl feature. Ulna and fibula are separate and complete, and the fibula ends freely as in Carnivora.

The tail appears to have been of some length. They were probably omnivorous animals and they varied from the size of a tapir to that of a fox.

This appears to be a central group with affinities to the Creodonta, Perissodactyla, and to the Hyracoidea. Affinities to the Insectivora and Primates have also been claimed by

Cope, so that, as it can hardly be supposed that we have found remains showing all the variations of structure characteristic of this order, it seems not unreasonable to conclude that the Condylarthra constituted a group combining characters now belonging to many mammalian groups and totally unlike any order now existing. If this view conveys a correct appreciation of the facts, it would seem unwise to pick out those of its features which show a faint resemblance to the Ungulata, and allow them to fix the position of the group in the system. We have therefore ventured to confer upon the Condylarthra ordinal rank.

*Periptychus* Cope, basal beds (Puerco Formation) of the Eocene of New Mexico, tarsal bones interlock. *Euprotogonia* Cope, L. Eocene of New Mexico, with interlocking carpalia, the tarsus appears to be serial. *Mioclaenus* Cope, L. Eocene of New Mexico, *Protoselene* Matthew, L. Eocene, N. Mexico. *Meniscotherium* Cope, L. Eocene of Mexico, carpus and tarsus serial. *Hyracops* Marsh, upper molars quadritubercular with W-shaped outer wall, and two ridge-like intermediate tubercles. *Pleurastoidotherium* Lemoine, L. Eocene, France. *Phenacodus* Cope, of which complete skeletons have been obtained from the Wasatch Formation of N. America; digitigrade with 15 dorsal vertebrae; upper molars with four principal and two intermediate tubercles; the two anterior premolars with one cusp, the two posterior with main cusp and one or two inner cusps.

The **Astrapotheridae** may provisionally be placed here. They are extinct forms from the Cretaceous and Eocene of Patagonia.

### Order 15. CREODONTA.\*

*Extinct, digitigrade or semiplantigrade, carnivorous animals with penta- or tetra-dactyle, clawed limbs. The canines are large, the dentition complete and the brain small and weakly furrowed. The carpus has a centrale, the femur a third trochanter, and the humerus usually an entepicondylar foramen. Eocene to the L. Miocene of Europe and North America.*

The Creodonta are frequently placed as a suborder of the Carnivora to which they present many resemblances, especially in the dentition; but they differ from them in the small size of the brain, the absence of carnassial teeth, and in the

\* Cope, *The Creodonta*, *Amer. Nat.*, 1885. Schlosser, *Die Affen, Lemuren, Chiropteren, Insectivoren, Marsupialier, Creodonten und Carnivoren des Europ. Tertiärs*, *Beitr. zur Palaeont. Oesterr.-Ung.*, 6, 1887, and 9, 1889. Osborn and Earle, *Bull. Amer. Mus. Nat. Hist.*, 7, 1895. Scott, *Revision of the N. Amer. Creodonta*, *Proc. Acad. Nat. Sc. Philadelphia*, 1892. Wortman, *Studies of Eocene Mammalia*, 1-4, *American Journal of Science*, 13 and 14, 1902.



separation of the scaphoid and lunar bones of the carpus. They also approximate closely to the Condylarthra, and show some resemblance to the Insectivora, and to the carnivorous Marsupials (through the Sparassodontidae, p. 540), but they differ from the latter in having a complete succession of teeth, and in being without the inflected angle of the lower and the palatal vacuities characteristic of that group. It is clear, therefore, that like the Condylarthra they are a central group with affinities in several directions, and that it is safest in the present state of knowledge to accord them independent ordinal rank.

In addition to the important characters already referred to, the following may be mentioned. The skull is carnivora-like and the muzzle usually elongated. The dentition is normal,  $i \frac{3}{3} c \frac{1}{1} p \frac{4}{4} m \frac{3}{3}$  or slightly reduced. The canines are powerful and sometimes two-rooted. The back-teeth are inclined to be trenchant, but the carnassial modification, so characteristic of Carnivora, is not found. The ulna and radius are separate, the carpus has a centrale and the scaphoid and lunar are not united. The terminal phalanges are often split and flattened at the ends. The lumbar region of the vertebral column is rigid owing to the form of the zygapophyses. They appear to have been, in some cases at least, semiaquatic. The principal genera are: *Arctocyon* Blv., a bear-like omnivorous form; *Mesonyx* Cope, a thylacine-like form; *Proiverra* Rüt.; *Sinopa* Leidy (*Stypolophus*); *Patriofelis* Leidy, a seal-like form; *Miacis* Cope; and *Hyaenodon* Luizer and Parieu, the most specialised and best known of the group.

#### Order 16. CARNIVORA \* (FISSIPEDIA).

*Carnivorous, sometimes omnivorous mammals with large projecting canine teeth, almost invariably three incisors on each side in each jaw, cutting premolars, and tuberculate molars. The last upper premolar and the first lower molar are always modified as carnassial teeth. The clavicles are absent or reduced, the scaphoid and lunar bones are fused, the limbs have never fewer than four digits and are unguiculate. The placenta-tion is zonary.*

The Carnivora are by no means all exclusively carnivorous; a considerable number are omnivorous and some chiefly

\* Gray, Carn., Pachyderm., and Edentate Mamm., *Brit. Mus. Cat.* 1869. C. Grevé, Die geograph. Distrib. de jetzt lebenden Raubthiere, *Nov. Act. k. Leop-Carol Deutsch. Akad. Naturf. zu Halle*, 63, 1893. Lydekker, *Carnivora* (Felidae and Viverridae) in Allen's Library, 1895. H. Winge, Jordfunde (Carnivora) fra Brasilien, cum appendice de class. etc., *E Museo Lundii*, 1895. See also Cope, *Amer. Nat.* 1880, p. 833, and 1883, p. 235. Flower, *P.Z.S.*, 1869, p. 5. Mivart, *P.Z.S.*, 1882, 1885.

vegetable feeders. The dentition though essentially similar throughout the group shows some variation which is generally correlated with the mode of nutrition, though in the case of the bears it would be difficult to distinguish the carnivorous forms from the frugivorous by this character alone.

The essential features are as follows : six incisors (very rarely fewer) in each jaw, conical or chisel-shaped, set nearly in a straight line across the jaw and usually increasing in size from within outwards ; two powerful pointed canines projecting beyond the other teeth ; a variable number of grinders divided as usual into premolars, which have predecessors in the milk dentition, and molars. The lower canines bite in front of the upper, which are separated from the

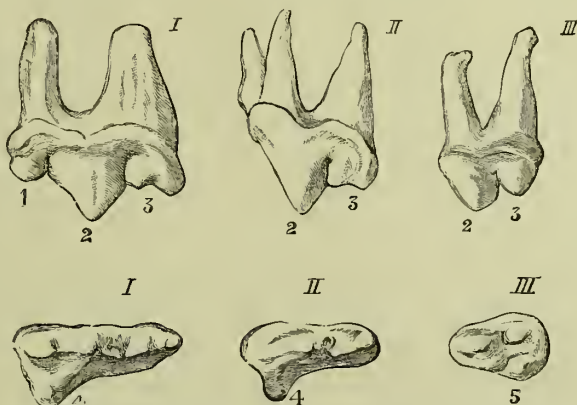


FIG. 322.—Left upper carnassial teeth I of *Felis*, II of *Canis*, III of *Ursus*, seen from the outer side and from below (from Flower and Lydekker). 1 anterior, 2 middle, 3 posterior cusp of the blade, 4 inner cusp of the upper carnassial, supported on distinct root, 5 inner cusp posterior in position and without distinct root, characteristic of the Ursidae.

incisors by a small gap. One of the grinding teeth on each side in each jaw is different from the rest and called the *carnassial* or *sectorial* tooth. In the upper jaw the tooth so modified is *p* 4, in the lower jaw *m* 1. The teeth in front of the carnassial are sharp and compressed, those behind it as a rule are broad and tuberculated. The former consist of a main cusp to which is frequently added a small anterior and posterior cusp. The carnassial tooth of the upper jaw (*p* 4) has when typically developed, an elongated trituberculate crown and three roots (Fig. 322, II). Two of these tubercles (2, 3), of which the anterior (2) is the longer, may be said to constitute the outer blade of the tooth, while the third is low (4) and forms a talon-like process at the anterior end of

the tooth ; the outer blade is supported on two roots and the inner cusp on one root. In the *Felidae* (Fig. 322, *I*), *Hyaenidae*, and some *Viverridae* there is an additional anterior outer tubercle (1), so that the blade is 3-cusped. In the *Ursidae* (Fig. 322, *III*) the inner tubercle and the corresponding root are absent, but there is often a small posterior inner cusp without root (5). The lower carnassial (*m* 1) has two roots and consists of an outer cutting blade with two cusps of

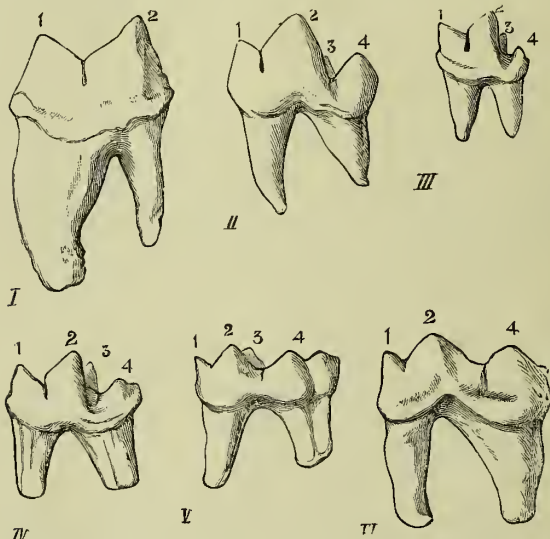


FIG. 323.—Left lower carnassial teeth *I* of *Felis*, *II* of *Canis*, *III* of *Herpestes*, *IV* of *Lutra*, *V* of *Meles*, *VI* of *Ursus* (from Flower and Lydekker). 1 anterior, 2 posterior cusp of the blade ; 3 inner cusp ; 4 talon.

which the posterior is the larger (Fig. 323, *II*, 1, 2), an inner tubercle (3) and a talon (4). In the *Felidae* the talon is not developed (Fig. 323, *I*), and the tooth is entirely a cutting tooth. In the omnivorous forms, e.g. *Ursus* (*I V.*), the talon is much developed

and tuberculated. The teeth behind the carnassial (molars) have broad crowns and are trituberculate in the purely carnivorous forms, tetra- or multi-tuberculate in the omnivorous forms. The more exclusively carnivorous the diet, the fewer and weaker are these teeth : in the *Felidae* there are none of them in the lower jaw and only one pair in the upper. From this account it will be gathered that in the purely carnivorous forms the cheek teeth are practically all sharp trenchant teeth, adapted for cutting the flesh off the bones of the animals on which they prey, whereas in the omnivorous or mainly vegetable-feeding species the posterior cheek teeth have broad and tuberculate crushing crowns.

The milk dentition is  $i \frac{3}{3} c \frac{1}{1} m \frac{3}{3}$  (except in the Felidae in which the deciduous molars are  $\frac{3}{2}$ ). The first deciduous molar  $dm$  1 is displaced by  $p$  2 of the permanent dentition,  $dm$  2 is displaced by  $p$  3 but resembles  $p$  4 (carnassial in the upper jaw),  $dm$  3 is displaced by  $p$  4 but resembles  $m$  1 of the permanent dentition.\* P 1 of the permanent dentition which has no deciduous predecessor and the anterior molar appear before any of the deciduous molars are shed.

The paroccipital process of the exoccipital projects either behind the bulla (Ursidae) or is closely applied to its hinder surface (Felidae, Viverridae). The mastoid process of the periotic is usually rather weakly developed. The opening for the carotid canal is either at the front end of the foramen lacerum posterius, or a little way in front of this on the inner side of the bulla. The condylar foramen for the hypoglossal may either be behind the foramen lacerum posterius or within its lips (Felidae). There is a postglenoid foramen for a vein just behind the glenoid cavity except in the Viverridae and living Felidae. The alisphenoid canal is present in Ursidae, and Canidae, and Viverridae, but absent in Mustelidae, Felidae, and Hyaenidae. In the older extinct Felidae, however, both alisphenoid canal and postglenoid foramen are present, and the condylar foramen opens behind the foramen lacerum posterius.

The orbit is not closed behind but the frontals carry post-orbital processes. The nasals are well developed. There is often a well-marked sagittal crest at the union of the parietals. The jugal is strong and the palate is completely ossified. The tympanic forms a flat or inflated bulla and may or may not be prolonged below the external auditory meatus. The mandible has a coronoid process, and the glenoid articulation of the lower jaw is transversely directed, thus restricting the motion of the jaw to the vertical plane.

The dorso-lumbar vertebrae are usually twenty in number. The clavicles are always reduced and sometimes absent. The humerus may or may not have an entepicondylar foramen, and the ulna and fibula are distinct. The scaphoid

\* It has been suggested that we have to do here with an overlapping of the premolar and molar series, similar to that suggested for the Marsupials (p. 530).



and lunar are fused in the carpus, and there is no centrale. The femur is without a third trochanter. The pollex and hallux are not opposable, and the digits are nearly always provided with sharp claws. The bears are plantigrade; the others either digitigrade or semidigitigrade (sub-plantigrade).

In some forms, particularly the Felidae, the claws are retractile. The retraction consists in the folding back of the ungual phalanx into an integumentary sheath, placed in the manus on the outer or ulnar side of the middle phalanx of the digit, in the pes on the dorsal surface\* of the corresponding phalanx; it is effected by an elastic ligament connecting the two phalanges. The straightening out of the phalanges and consequent protrusion of the claws is caused by the contraction of the flexor profundus digitorum muscle.

The cerebrum is fairly large and usually well convoluted, but it never completely covers the cerebellum.

The stomach is simple and the large intestine is generally provided with a caecum (absent in Ursidae) which is however short.

The testes descend into a scrotum, and there is generally an os penis. The glans penis, which is frequently covered with recurved hooks, swells in some forms (e.g. Canidae) during the act of copulation so that it cannot be withdrawn. Vesiculae seminales are always absent, and Cowper's glands are present or absent.

The ovaries are contained in peritoneal sacs and the uterus is bicornuate. The mammae are abdominal or thoracic and the placenta is always zonary.

The living Carnivora may be classified in three sections, the cat-like or *Aeluroidea*, the dog-like or *Cynoidea* and the bear-like or *Arctoidea*. The characters utilised are taken from certain features of the base of the skull around the tympanic region and agree fairly well with the characters afforded by the dentition and other parts of the body.

The *Aeluroidea* including the Felidae, Viverridae, Hyaenidae and Protelidae present the following features. The auditory bulla is dilated and nearly divided into two chambers by a septum; the lower lip of the bony auditory meatus is very short; the paroccipital process is closely applied to the

\* And to a certain extent on the fibular side.

bullæ, and the mastoid process is inconspicuous or absent; the condylar foramen opens within the margin of the foramen lacerum posterius and the postglenoid foramen is absent; the alisphenoid canal is absent. The opening of the carotid canal in the Felidae looks into the foramen lacerum posterius, but it and the foramen lacerum medium are very minute in accordance with the small size of the internal carotid artery. In other Aeluroidea the carotid canal is a groove at the side of the bullæ, and the foramen lacerum medium is better marked. The molars are reduced; there is a short caecum; the os penis is small or absent. Cowper's glands are present.

The *Cynoidea* include the Canidae. The bullæ is inflated, but the internal septum is very incomplete. The lower lip of the external auditory meatus is longer than in the cats. The paroccipital process is applied to the back of the bullæ, but its end is free. The condylar foramen is distinct from the foramen lacerum posterius and there is a postglenoid foramen. The alisphenoid canal is present and the posterior opening of the carotid canal looks into the foramen lacerum posterius. The molars are less reduced, and the blade of the upper carnassial has two cusps. The caecum is folded, the os penis is present and grooved, and the male is devoid of Cowper's glands.

The *Arctoidea* include the Ursidae, Procyonidae and Mustelidae. The bullæ is without a septum and usually flattened; there is a considerable lower lip to the bony auditory meatus. The paroccipital process stands behind and clear of the bullæ; the mastoid process is prominent. The condylar foramen is distinct from the foramen lacerum posterius and there is a postglenoid foramen. The alisphenoid canal is absent except in *Ursus*, *Melursus* and *Aelurus*, and the posterior opening of the carotid canal is placed on the inner margin of the bullæ behind the foramen lacerum posterius. The molars are as in the dogs but the crowns are broad and tuberculated, and the carnassial teeth differ (except in *Mustelidae*) from those of the other two sections; there is no caecum; the os penis is large and not grooved; Cowper's glands are absent and the prostate is small; there are always five completely developed toes on each foot.

These divisions, though very convenient when applied to living forms, break down when the extinct species are considered. Thus, as already mentioned, in the older extinct *Felidae* the alisphenoid canal and postglenoid foramen are both present, the condylar foramen opens behind the foramen lacerum posterius, and the molars are more numerous. Moreover some of the older *Viverridae* seem to approach so close to the *Mustelidae* both in their cranial and dental characters that it is difficult to separate the two families. The inference has been drawn from these facts that the *Arctoidae* are not a natural group and that the resemblances between the living *Mustelidae* and *Ursidae* have been independently acquired. This conclusion is not in our opinion justified. To say that features of resemblance which undoubtedly exist between two families A and B, have been independently acquired simply because A is found to present features of resemblance to a third family C, which B does not resemble so closely, seems to us an unsatisfactory position for a systematic zoologist to hold. We should prefer to leave out all speculations as to descent and to place the matter in this way. Certain extinct animals (e.g. *Stenoplesictis*, etc.) must be placed with the living *Felidae* and *Viverridae* because of certain characters, but they differ from these living forms in also possessing characters which belong to *Mustelidae*. These however are not strong enough to separate them from the living *Felines*, but are only sufficient to show a closer affinity of *Felines* to *Mustelidae* than was at first thought possible. In the same way the *Mustelidae* have certain *Ursine* features which induce us to class them with bears. These are on the whole more important than the resemblances to the extinct *Felines*, so we leave the *Mustelidae* with the *Ursidae*, merely noting the fact that they have affinities to the extinct *Felines*. What we have here is merely an example of the principle, to which we have often before called attention in this work, that the more closely any given group of animals is studied, the more complex are the mutual relations between its different members found to be. For an example of this we may refer the reader to vol. I, p. 410. We have there given a rough diagram showing the interconnections existing between different groups of the *Nudibranchiata*. A similar diagram might be constructed in the present case.

## AEUROIDEA.

Fam. I. **Felidae**.<sup>\*</sup> Dentition  $i \frac{3}{3} c \frac{1}{1} p \frac{4}{4} - \frac{2}{2} m \frac{1}{1-2}$ ; canines very strong; upper carnassial with three lobes on the blade and an inner cusp (Fig. 322), lower with two outer cusps (Fig. 323), a weak or absent inner cusp, and a weak cutting or absent talon. U. molar very small and transverse. Premolars reduced in number. Auditory bulla inflated, with an internal septum and short bony auditory meatus, the paroccipital processes flattened against the bulla; without alisphenoid canal †; carotid canal minute; condylar foramen within foramen lacerum posterius. The humerus has an entepecondylar foramen. Digitigrade, manus with 5, pes usually with 4 digits. Os penis small, Cowper's glands present, prostate

<sup>\*</sup> Elliott, *Monograph of the Felidae*, London, 1878-83. Mivart, *The Cat*, London, 1881. Cope, The extinct cats of America, *Amer. Nat.*, 1880, p. 833. Adams, Extinct *Felidae* of N. America, *Amer. Journ. Sci.*, 1, 1896, p. 419.

† Present in some extinct forms.

lobed. The Felidae are distributed over the whole world save in Australasia and Madagascar. Their fossil remains first appear in the Upper Eocene, and give us no clue to the origin of the family. *Felis* L.,  $i \frac{3}{8}$   $c \frac{1}{2}$   $p \frac{3}{8}$   $m \frac{1}{2}$ , lower carnassial without talon and inner cusp, upper molar small, the first upper premolar ( $p$  2) may be absent; clavicles better developed than in other Carnivora, claws very retractile, tongue with sharp horny papillae; 50 living species, Neotr. 13, Ethiopian 8, Oriental 15, Nearct. 7, Pal. 20; fossil in the M. Miocene onwards. *F. leo*, lion, Afr., India, W. Asia. *F. tigris*, tiger, nasal bones reach back beyond the frontal processes of the maxillae, Asta, Sumatra, Java, not Ceylon. *F. pardus*, leopard, pard. Afr. and Asia, Ceylon, Java, Sumatra, Borneo. *F. uncia*, ounce, highlands of C. Asia. *F. nebulosa*, clouded leopard, S.E. Asia, Sumatra, Java, Borneo, Formosa. *F. serval*, serval, S. Afr. *F. catus*, wild cat of Eur., British. *F. caffra*, caffre cat, Afr. and S. Asia, the domestic cat is probably derived from this species. *F. caracal*, caracal, India, Persia, Arabia, Africa. *F. lynx*, lynx, stumpy tail, lower carnassial with trace of talon Scandinavia, Russia, N. Asia. *F. concolor*, puma, Amer. from Canada to Patagonia. *F. onca*, jaguar, Amer. from Texas nearly to California. *F. pardalis*, ocelot, tiger-cat, trop. Amer. *Cynaelurus* Wagler, with 1 sp., *Cynaelurus jubatus*, the cheeta or hunting leopard, same distribution as the lion, claws less retractile, talon of upper carnassial without cusp. Several fossil genera are allied here, some placed in separate families; *Proaelurus*, *Aelurictis*, *Dinictis*, *Pogonodon*, *Hoplophonus*, etc.; *Machaerodus*, the sabre-toothed tiger with enormous upper canines, upper Eocene to Pleistocene of Europe and Miocene of India, *Smilodon*, a similar form from Pleistocene of America. It is remarkable to find these large and highly specialised carnivora suddenly appearing and flourishing as far back as the Eocene.

Fam. 2. **Viverridae.** Civets, genets; comparatively small animals with long bodies and heads;  $p \frac{3}{8}$   $cr \frac{1}{4}$   $m \frac{1}{2}$  or  $\frac{3}{4}$ ; upper carnassial usually with two, sometimes with three outer cusps, and an inner cusp at the front end; lower carnassial with two outer and an inner cusp and a well-developed, cusped talon; upper molars tritubercular. Auditory bulla with septum. Usually an alisphenoid canal. Carotid canal has a groove on the side of the bulla. Humerus usually with an entepicondylar foramen. Plantigrade or digitigrade; usually pentadactyle, but pollex and hallux may be absent; usually with well-developed perineal scent glands. They are found in the Old World including Madagascar, but not in Australasia. They are not found either living or extinct in the New World. There are about 26 genera and 69 species. They are known fossil from the Upper Eocene onwards. The dentition is primitive in the large number of premolars. The upper carnassial essentially resembles that of the Canidae and Mustelidae, and the upper molars resemble those of the Canidae. The lower carnassial resembles that of the older extinct Canidae and Mustelidae, and were it not for the third lower molar of the Canidae it would be impossible to distinguish the lower jaw of the older Canidae and Viverridae. In the elongation of the skull and its construction behind the orbits the two families are alike and are supposed to be primitive. In fact it seems clear that the Viverridae of the present day resemble in some important features the older Canidae and Mustelidae.

*Cryptoprocta* Bennett, sometimes placed with the Felidae on account of its dentition, which is feline;  $i \frac{3}{8}$   $c \frac{1}{2}$   $p \frac{3}{8}$   $m \frac{1}{2}$ ;  $p$  1 is minute and transient, the upper carnassial has a small inner cusp; molar small and placed



transversely as in Felidae; lower carnassial without inner cusp, with a minute talon; subplantigrade, pentadactyle; Madagascar 1 sp., *C. ferox*; shows some affinity to the extinct Felines, *Proaelurus*, and *Pseudaelurus Viverra* L., civets, include the largest species, preineal glands well developed and yielding the civet used in perfumery, Ethiopian 1 sp., Oriental 4 sp., *V. civetta*, African civet; *V. zibetha*, Indian civet. The genus *Viverra* is known from the Eocene. *Viverricula* Hodgs., rasse, 1 sp. Oriental and Madagascar; *Fossa* Gray, Madagascar 1 sp., without scent pouch; *Geneta* G. Cuv., genets, Ethiop. 4 sp., Pal. 1 sp., *G. vulgaris* in France s. of the Loire, also Asia and Afr.; *Prionodon* Horsf., linsangs, 3 sp., Oriental, without the second upper molar; *Poiana* Gray, 1 sp., Ethiop.; *Paradoxurus* F. Cuv., palm-civets, 10 sp., Oriental, some of the species vary their diet with fruit; *Arctogale* Gray, Oriental 2 sp., *Hemigale* Jourd. Orient. 2 sp.; *Arctictis* Temm., binturong, arboreal, partly vegetable feeders, 1 sp. Orient.; *Nandinia* Gray, 2 sp. Ethiop., without caecum and hinder part of bulla unossified; *Cynogale* Gray, 1 sp. Orient., semiaquatic and arboreal, feeding on fish, small mammals, birds and fruit. *Herpestes* Ill., ichneumons, mongooses,  $p \frac{1}{4}$  or  $\frac{3}{8}$ ,  $m \frac{2}{2}$ ; pentadactyle, plantigrade, postorbital process of frontal and jugal generally meeting, feed on small mammals, birds, reptiles, eggs of birds and reptiles, insects, famous as snake destroyers, 9 sp. Orient., 10 sp. Ethiop., 1 sp. Pal., *H. ichneumon* is found in Europe, *H. mungo* the common Indian mongoose; *Helogale* Gray, Afr. 2 sp.; *Bdeogale* Pot., Afr. 2 sp.; *Cynictis* Ogilv., Afr. 2 sp., with long caecum; *Rhinogale* Gray., Afr. 1 sp.; *Crossarchus* F. Cuv., Afr. 5 sp.; *Suricata* Desm., meerkat, Afr. 1 sp. The three next genera are from Madagascar and are distinguished by the absence of alisphenoid canal and entepicondylar foramen. *Galidictis* Geoffr., 2 sp., *Galidea* Geoffr., 1 sp., *Hemigalidea* Doyère, 2 sp. *Eupleres* Jourd., 1 sp. Madagascar, with weak jaws and small teeth; on account of these it was included among Insectivora; with entepicondylar foramen, without alisphenoid canal. Extinct genera: *Amphictis*, Upper Eocene (with *Viverra*), *Ictitherium*, Upper Miocene.

Fam. 3. **Protelidae**. Without alisphenoid canal, auditory bulla divided into two chambers, pes with 4, manus with 5 toes; premolars and molars  $\frac{4}{3 \text{ or } 4}$ , small, placed far apart and simple; feed on insects and carrion. *Proteles* Geoffr., 1 sp., *P. cristatus*, aard wolf of S. Africa; a burrowing nocturnal animal. This family is sometimes united with the next.

Fam. 4. **Hyaenidae**.\*  $i \frac{3}{3}$   $c \frac{1}{1}$   $p \frac{2 \text{ or } 4}{3 \text{ or } 4}$   $m \frac{1}{1-2}$ ; upper carnassial elongated, with three outer cusps and an inner cusp at the front end, lower carnassial with two cusps and weak talon; upper molar small, placed transversely within the line of the other grinders; bulla without septum, alisphenoid canal absent; humerus without entepicondylar foramen; digitigrade, manus usually, pes always with 4 toes; hind limbs shorter than fore. They are apparently related to the Viverridae through *Ictitherium* of the Upper Miocene of Eur., and India. There is one living genus confined to the Old World, 3 sp. Ethiop., 1 sp. Afr., and 1 sp. Pal.; fossil genera (*Hyaenictis*, etc.) from the Miocene onwards of Eur., N. Afr., S. Asia. *Hyaena* Zimm.,  $p \frac{4}{4}$ ,  $m \frac{1}{1}$ , mainly carrion eaters; *H. crocuta* the spotted hyaena, Afr., S. of Sahara; *H. striata* the striped hyaena of N. Afr., and S. Asia.

\* Watson, *P.Z.S.*, 1877, 78, 79, and 81, on visceral anatomy of hyaenas.

## CYNIOIDEA.

Fam. **Canidae** \*  $i \frac{3}{3}$   $c \frac{1}{1}$   $p \frac{1}{1}$   $m \frac{2+2+3}{3}$ ; upper carnassial elongated with two outer cusps and inner cusp at the front end; upper molars three-cusped, transversely elongated, often with intermediate cusps; lower carnassial ( $m 1$ ) with two outer cusps and a small inner cusp placed just behind the posterior of the two outer, and a broad tuberculated talon;  $m 2$  smaller,  $m 3$  very small. The bulla is inflated and undivided, the septum being incomplete and small, the tympanic is prolonged a short distance as the floor of the external auditory meatus; the paroccipital process in contact with bulla, but long. The condylar foramen is outside the foramen lacerum posterius and the carotid canal is present. There is an alisphenoid canal. Entepicondylar foramen absent in living species, but present in the older fossil forms. Digitigrade, manus 4- or 5-toed, pes usually 4-toed, claws not retractile; a considerable os penis. Caecum small, but always present, and generally folded. The Canidae are found in all the great regions excepting New Zealand and Madagascar. They are supposed by some to be the most primitive of existing Carnivora. The occasional presence of traces of epipubic bones and of an inflection of the angle of the lower jaw (*Otocyon*) may be mentioned in connection with this view. They first make their appearance in the Upper Eocene of Europe, and their remains are found in the Miocene, Pliocene, and Pleistocene of Europe, Asia and N. America, in the Pliocene and Pleistocene of S. America and in the Pleistocene of Australia. *Canis L.*,  $i \frac{3}{3}$   $c \frac{1}{1}$   $p \frac{1}{1}$   $m \frac{2}{2}$ , but the dentition is slightly variable,  $m 3$  in the upper jaw is occasionally present, and  $m 3$  in the lower is occasionally absent; milk dentition,  $i \frac{3}{3}$   $c \frac{1}{1}$   $m \frac{3}{3}$ , the first permanent premolar has no predecessor. Vertebrae C7, D13, L7, S3, C17-22. Clavicles reduced, manus with 5 toes, pollex very short, pes with 4 toes and the metacarpal of the hallux (occasionally with loose small phalanges and claws in domestic dog). They generally hunt in packs. Some burrow. All are carnivorous, but some species may eat insects and vegetables.

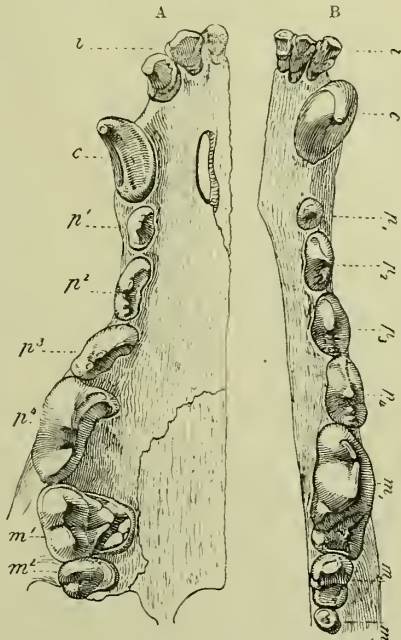


FIG. 324.—*Canis lupus*. A right upper jaw, B right lower jaw  $\times \frac{2}{3}$  (from Zittel).

\* Huxley, Dental and cranial characters of the Canidae, *P.Z.S.*, 1880, p. 238. Mivart, *Monograph of the Canidae*, 1890.

The distribution is that of the family. The genus dates from the Miocene,\* or possibly even from the Eocene.† There are 35 species which may be divided into the fox-like and the wolf-like, Aust., 1 sp. (*C. dingo*), Neotrop. 9 sp., Ethiopian 7 sp., Oriental 3 sp., Nearct. 9 sp., Pal. 13 sp. *C. lupus*, wolf, Pal. and Nearct., extinct in England since 1660, in Ireland since 1770; *C. aureus*, jackal, Pal. and Orient.; *C. rutilans*, *dukhunensis*, *javaanicus*, wild dogs of S.E. Asia; *C. cancrivorus*, *brasiliensis*, etc., wild dogs of S. Amer.; *C. latrans*, the prairie wolf; *C. dingo*, the Australian dingo, supposed by some on no particular grounds to have been introduced by man; *C. vulpes*, common fox, with other species; *C. lagopus* the arctic fox, changing colour to white. The origin of the domestic dogs is unknown. Probably they have originated from several wild species in different parts of the world. They have long been domesticated, and many primitive peoples at the present time possess them. The mental qualities which fit them to be the companion of man seem to be possessed in varying degrees by more than one species of the genus. *Lycaon* Brookes, 1 sp. S. Afr., *L. pictus* the Cape hunting dog. *Icticyon* Lund, 1 sp., S. Amer., *I. venaticus*, bush dog,  $m \frac{1}{2}$ . *Otocyon* Licht.,  $p \frac{1}{4}$   $m \frac{3 \text{ or } 1}{4}$ , 1 sp. *O. megalotis* S. Afr.

There are several extinct genera, *Cynodictis*, *Temnocyon*, *Galecyon*, *Amphicyon*, *Dinocyon*, *Simocyon*. Some of these connect the *Canidae* with the *Viverridae* and *Ursidae*.

In *Cynodictis*, U. Eocene, Europe, the dental formula is as in *Canis*, the teeth like those of the *Viverridae*; the auditory bulla is inflated and without septum and there is an entepicondylar foramen. *Amphicyon* L. and M., Miocene, Europe, on the other hand is dog-like by its dentition but approaches the *Ursidae* by its limbs which are pentadactyle and plantigrade.

## ARCTOIDEA.

Fam. 1. **Ursidae.** Dentition with some slight variations is  $i \frac{3}{4}$   $c \frac{1}{4}$   $p \frac{1}{4}$   $m \frac{2}{3}$ ; the carnassial teeth differ from those of the dogs and cats; the upper carnassial ( $p \ 4$ ) with two outer cusps and an inner posterior cusp without a separate root; the anterior premolars small transient and sometimes absent; upper molars quadratic or oblong with multituberculate crowns, the last is the largest; in the lower jaw the three anterior premolars are small and may fall out early as in the upper, the carnassial ( $m \ 1$ ) is elongated, the front part has three cusps and there is a large tuberculated talon;  $m \ 2$  is multituberculate and larger than  $m \ 1$ ,  $m \ 3$  is smaller than either. The milk teeth are small and shed early. The skull is rather elongated. The tympanic bulla is depressed, and there is no septum; the tympanic is prolonged for a considerable distance on the floor of the external auditory meatus, the paroccipital process is separate from the mastoid process; the condylar foramen is distinct from the foramen lacerum posterius; the carotid foramen is large and placed on the inner margin of the bulla, the alisphenoid canal is present except in *Aeluropus*. Plantigrade; pentadactyle, with short tail and large os penis. The humerus is without entepicondylar foramen. There is no caecum, and the kidneys are lobate. They are large omnivorous carnivores which feed on flesh, fruits, roots, honey, etc., and are distinguished from all other

\* Scott, *Trans. Am. Phil. Soc.* 18, 1894, p. 75.

† Marsh, *Amer. Journ. Sci.*, 1871, p. 123.

carnivores by their multituberculate molars and carnassial teeth. They are found in all regions except the Ethiopian and Australasian, and Madagascar. They make their appearance in the Miocene, and are closely connected with the Canidae by the extinct genus *Amphicyon*. *Ursus* L., bears, animals of considerable bulk,  $p \frac{4}{3}$ ,  $m \frac{3}{2}$ , vertebrae, C7, D14, L6, S5, C8-10; claws curved and non retractile; the three anterior premolars in both jaws small and one-rooted, sometimes absent,  $p$  1 of the lower jaw is small, separated by a wide gap from  $p$  2 and soon falls out; 10 sp., viz. Neotrop. 1, Orient. 2, Nearct. 4, Pal. 5. Omnivorous or herbivorous. *U. maritimus* polar bear, circumpolar; *U. arctos* brown bear, Pal. region, is still found in Europe in the Pyrenees, Norway, Hungary and Russia; *U. horribilis*, grizzly bear of N. Amer.; the genus is first found fossil in the Pliocene. *Melursus* Meyer, sloth bear first upper incisors shed early or absent, with small teeth, feeds on insects, fruit, honey; 1 sp., *M. labiatus*, India, Ceylon. *Aeluropus* M. Edw.,  $p \frac{4}{3}$   $m \frac{3}{2}$ ; 1 sp. *A. melanoleucus* in Thibet, a large herbivorous animal with large and multicuspid, two-rooted (except the first) premolars. There are a few extinct genera, e.g. *Arctotherium*, *Hyænartcos*.

Fam. 2. **Procyonidae.**  $i \frac{3}{2}$   $c \frac{1}{2}$   $p \frac{4}{3}$   $m \frac{3}{2}$ ; carnassial teeth not typically developed, molars broad and tuberculate, upper  $p$  4 quadrilobulate and like the molars; lower molars quadrangular with two-cusped talon. Alisphenoid canal absent except in *Aelurus*. Tympanic bulla (sometimes rather inflated) and adjacent parts as in the Ursidae. Tail long. Entepicondylar foramen present or absent. Feet pentadactyle, plantigrade. Omnivorous. Confined to America save for the genus *Aelurus* which is Oriental. A few fossil species in the Pleistocene of America. *Aelurus* F. Cuv., the panda,  $p \frac{3}{4}$   $m \frac{2}{3}$ ,  $p$  1 of the lower jaw small and early deciduous, molars broad and tuberculate, mainly a vegetable feeder; 1 sp. *A. fulgens*, rather larger than a cat with thick fur, S.E. Himalaya. *Procyon* Storr, racoons,  $p \frac{4}{3}$   $m \frac{3}{2}$ , longish limbs, manus remarkable for handiness and the great mobility of its digits, omnivorous, 2 sp., *P. lotor*, dips its food in water before eating, N. Amer.; *P. cancrivorus*, S. Amer. *Bassariscus* Rhoads, 1 sp., U.S. and C. Amer. *Bassaricyon* Allen, 2 sp., S. Amer. *Nasua* Storr, coati-mundis, arboreal, 2 sp. in N. and S. Amer. *Cercoleptes* Ill., the kinkajou, arboreal, in forests, 1 sp., N. and S. Amer.

Fam. 3. **Mustelidae.** Weasels, badgers, otters. For the most part bloodthirsty animals with elongated bodies;  $i \frac{3}{2}$   $c \frac{1}{2}$   $p \frac{4}{3}$   $m \frac{1}{2}$ ; upper carnassial ( $p$  4) with two sharp outer cusps, and strong inner cusp; lower carnassial ( $m$  1) large, with large often excavated talon; upper molar broad, tritubercular,  $m$  2 in the lower jaw small, soon falling out. Tympanic bulla and adjacent parts as in Ursidae except that the bulla may be swollen and the paroccipital process pressed against it; alisphenoid canal absent. Feet usually pentadactyle, plantigrade or digitigrade. Entepicondylar foramen present or absent. The kidneys are lobed in the otters. They are universally distributed, being absent only in the Australian region and in Madagascar. There are 17 living genera which may be divided into the otter-like (*Lutrinae*) the badger-like (*Melinae*) and the weasel-like (*Mustelinae*). The family is known from the Upper Eocene of Europe onwards. Some of the extinct genera show a close approximation to the earlier Viverridae and can scarcely be separated from them. *Stenoplesictis* with a dentition of  $i \frac{3}{2}$   $c \frac{1}{2}$   $p \frac{4}{3}$   $m \frac{3}{2}$ , and a complete septum in its bulla has even been placed with the Viverridae. Other genera are *Palaeoprionodon*, *Haplogale*, *Stenogale*, *Plesictis*—all Upper Eocene, and (some of them)



Lower Miocene. *Mustela* and *Lutra* make their appearance in the Middle Miocene.

Sub-fam. 1. **Lutrinae**. Otters. With webbed toes, and lobed kidneys, aquatic. *Lutra* Ill.,  $i \frac{3}{3} c \frac{1}{1} p \frac{4}{3} m \frac{1}{2}$ ; 11 sp., Neotrop. 3, Ethiop. 2, Orient. 3, Nearct. 2, Pal. 1; feed on fish; *L. vulgaris* the common British otter. *Latax* Gloyer (*Enhydra*),  $i \frac{3}{2} c \frac{1}{1} p \frac{3}{3} m \frac{1}{2}$ , the first lower incisor being absent: pes fin-like, phalanges flattened, 1 sp., *L. lutris* the sea otter, Nearctic, on the shores of the N. Pacific Ocean, feed on shell fish.

Sub-fam. 2. **Mellinae**. Badgers, etc. Feet elongated, claws non-retractile, terrestrial and fossorial. *Mephitis* Cuv., skunks,  $i \frac{3}{3} c \frac{1}{1} p \frac{3}{3} m \frac{1}{2}$ ; with largely developed anal glands, the secretion of which is extremely offensive, 5 sp. Nearctic, mainly insectivorous. *Conepatus* Gray, Neotrop. 3 sp., Nearct. 1 sp. *Arctonyx* F. Cuv., Orient. 1 sp., Pal. 3 sp.; *Mydaus* F. Cuv., Orient., 2 sp.; *Meles* Storr, badgers,  $i \frac{3}{3}, c \frac{1}{1} p \frac{4}{4} m \frac{1}{2}$ ; 4 sp., Pal.; *M. taxus*, the common badger of England, Europe and N. Asia, omnivorous. *Taxidea* Waterh., badgers of N. America, Nearct. 2 sp.; *Mellivora* Storr, the ratel, Ethiop. 1 sp., Orient. 1 sp.; *Helictis* Gray, Orient. 5 sp.; *Ictonyx* Kaup, 4 sp., Ethiop. 3, Pal. 2.

Sub-fam. 3. **Mustelinae**. Weasels, etc. Toes short, partially webbed; claws short, sharp, often semiretractile; terrestrial and arboreal. *Galictis* Bell, 2 sp., Neotrop.; *G. vittata*, the grison; *Mustela* L., martens and sables,  $i \frac{3}{3} c \frac{1}{1} p \frac{4}{4} m \frac{1}{2}$ ; 10 sp., Orient. 4, Nearct. 3, Pal. 5; *M. martes* pine-marten, arboreal, British N. Eur., Asia; *M. zibellina* the sable, E. Siberia; *M. americana*, the North American sable. *Putorius* Cuv., about 47 sp., Neotrop. 9, Orient. 15, Nearct. 16, Pal. 10;  $p \frac{3}{3}$ , includes the minks, weasels, ermines, stoats, ferrets, polecats; *P. vison*, mink of N. Amer.; *P. putorius*, the polecat, of which the ferret is a domesticated variety, British and European; *P. vulgaris*, the weasel, reddish-brown above, white below, British, Eur., Asia, N. Amer.; *P. erminea*, stoat or ermine, reddish brown above, white below, in some localities changing to white in winter except black tip of tail, larger than the weasel, British Eur., Asia, N. Amer.; *P. hibernicus*, the Irish stoat, confined to Ireland. *Poecilogale* Thos., S. Afr. 1 sp.; *Lyncodon* Gervais, 1 sp., Patagonia; *Gulo* Storr, the glutton or wolverine, 1 sp., circum-polar, Nearct. and Pal., has a habit of secreting articles which are of no use to it, mainly feeds on carcasses.

## Order 17. PINNIPEDIA.\*

*Aquatic Carnivora with pentadactyle fin-like limbs, the digits of which are united by a membrane. The brain is large and the cerebrum complexly convoluted.*

These animals are closely related to the Carnivora, from

\* Allen, *History of North American Pinnipeds*, 1880. Mivart, *Notes on the Pinnipedia*, P.Z.S., 1885, p. 484. van Beneden, *Ossem. fossiles d'Anvers*, *Mém. Acad. Roy. Belgique*, 1, 1877. Turner, *Report on the Seals of the "Challenger," Chall. Reports*, 26, 1887. Balkwill, *Geograph. Dist. of Seals, Zoologist*, 12, 1888, p. 401.

which they differ mainly in their dentition, aquatic habits and the structure of their limbs. The limbs are short and pentadactyle, the proximal portions being more or less imbedded in the common integument of the body. All the digits are united by a membrane which may or may not project beyond their extremities. Nails are occasionally well developed, but generally small or even absent. They are all covered with hair, and there is sometimes a fine soft under-fur, which in the fur seal is much developed. The incisors vary in number and are conical; they are never less than  $\frac{2}{2}$ . The canines project though not as much\* as in the Carnivora. The premolars and molars are all alike, and may be conical and one-rooted, or laterally compressed with three cusps and two roots; their number varies from five to six. The milk teeth are  $i \frac{3}{3}$ ,  $c \frac{1}{1}$ ,  $m \frac{3}{3}$  and are shed early, either before or shortly after birth. The cranium is generally rounded and capacious. The orbits are open behind and there is no lacrymal bone or canal. The tympanic bulla is large and is prolonged beneath the meatus auditorius; the paroccipital and mastoid processes are inconspicuous. The condylar foramen is distinct from the foramen lacerum posterius, and an alisphenoid canal is present or absent. The mandible has a coronoid process. The tail is short. Clavicles are absent; the scapula is large, the spine being nearer the hinder edge. The humerus is short and without entepicondylar foramen. Ulna and radius are separate, and the scaphoid and lunar are fused. The calcaneum has a short tuber calcis. There is always a considerable *os penis*. The brain is large and well convoluted, the olfactory nerves and anterior commissure small. The colon has a short caecum. The kidneys are lobulated, and Cowper's glands are absent. The mammae, two or four in number, are abdominal. A scrotum may be present or absent.

They are all aquatic, but come to the land, on which they move clumsily, to breed. They are mainly marine, but some species ascend rivers, or inhabit inland seas and lakes. Their fossil remains are found in Europe and North America from the Miocene onwards.

There can be no doubt that the Pinnipedia are allied to

\* Except in the walrus.

the Carnivora, and affinities especially with the Ursidae have been claimed through the Otariidae.

**Fam. Otariidae.** Eared seals. This family is characterised by possessing a small pinna, and by the fact that the hind limbs are capable of supporting the body in locomotion, being turned forwards beneath it. They have tolerably long necks, and the nostrils are placed at the end of the snout. The skin of the feet is extended beyond the nails, which are small, being best developed on the three middle digits of the pes. The skull has large post-orbital processes, and an alisphenoid canal. The angle of the lower jaw is markedly inflected. Vertebrae, C7, D15, L5, S4, C9-14. Dentition,  $i \frac{3}{2} c \frac{1}{1} p \frac{4}{4} m \frac{1+2}{1}$  of which  $p$  2, 3 and 4 are preceded by milk teeth, which are shed a few days after birth. The testicles descend into an external scrotum. They pair and bring forth their young on land, upon which they can move with considerable freedom. They are gregarious and polygamous. *Otaria* Pér., 9 species, principally Antarctic, but extending to the north in the Pacific; *O. stelleri*, the northern sea-lion, N. Pacific, about 10 feet in length. *O. jubata*, the Patagonian sea-lion from Patagonia and the Falkland Islands. *O. californiana* from California. *O. ursina*, the fur seal of commerce or sea-bear, with a dense soft under-fur, N. Pacific. *O. pusilla*, Cape of Good Hope. *O. forsteri*, Australia.

**Fam. Trichechidae.** Walrus or morse, with one genus *Trichechus* L. They are without external ears, but resemble *Otaria* in the position of their hind limbs and mode of walking. They are exceedingly bulky animals, and attain to a length of from 10 to 11 feet. The upper canines are modified into projecting tusks. They are covered with short hair, which tends to fall off in old age, and there is a tuft of long bristles on each side of the muzzle. The tail is reduced. The manus has sub-equal digits and small flattened nails; in the pes the nails of digits 1 and 5 are minute; those of the others large, compressed and pointed. The soles of the feet are devoid of hair and provided with a rough warty pad. The functional dentition is  $i \frac{1}{0} c \frac{1}{1} p$  and  $m \frac{3}{3}$ ; the molars are conical but wear down to flat crowns; in the young the teeth are  $i \frac{3}{3} c \frac{1}{1} m \frac{3}{3}$ , some of which are lost early or remain through life concealed beneath the gums. Vertebrae C7, D14, L6, S4, C12. The skull is round with an alisphenoid canal but without postorbital processes. There is a third bronchus on the right side, as in bears, ruminants and cetaceans. The cerebrum is large and richly convoluted, and there is a trace of a posterior cornu. They are gregarious and live on various shell fish, which they dig up with their tusks. They are much hunted for their skins, oil and ivory, and are rapidly diminishing in number and range. The distribution is circumpolar and there are two species, *T. obesus* in the N. Pacific, and *T. rosmarus* in the N. Atlantic.

**Fam. Phocidae.** Seals. More modified for an aquatic life than the preceding families. The nostrils are dorsal and there is no pinna, and the hind limbs are stretched out backwards on each side of the tail with which they are connected; they cannot be used in locomotion on land. The fore-limbs are buried to the elbow in the skin but can be used for supporting the body. The outer digits of the pes are longer than the middle. The under side of both manus and pes is hairy. There is no woolly under-fur. Both postorbital processes and alisphenoid canal

are absent, and the angle of the mandible is not inflected. The tympanic bullae and mastoid processes are large. The skull in many of its features recalls the cetacean type. Dentition,  $i \frac{3 \text{ or } 2}{2 \text{ or } 1} c \frac{1}{1} p$  and  $m \frac{5}{5}$ ; the canines are well developed; the milk molars appear to be  $\frac{3}{3}$ , and are sometimes shed during foetal life. There is no scrotum, and the testes are abdominal or just outside the inguinal canal.

Locomotion on the land is effected by a wriggling of the trunk, with or without the assistance of the forelimbs. They are inoffensive creatures and mostly gregarious and polygamous. They are exceedingly intelligent and docile, and in captivity attach themselves to man. It is said that in some species the young do not readily take to water, and have to be taught to swim. When born they have a thick soft fur, which falls off before they enter the water. They are much hunted for their skins and oil.

There are 9 genera and about 15 species, principally confined to the Arctic and Antarctic seas, but found in intermediate areas. Most of them are marine, but a few ascend rivers and are found in inland seas and lakes, as the Caspian and Lake Baikal. Their remains, not numerous, are known fossil from the Miocene onwards in Europe and N. America.

Sub-fam. 1. **Phocinae.**  $i \frac{3}{2}$ , feet with well-developed claws, digits of pes sub-equal with membrane not extending beyond the toes. *Halichoerus* Nils., 1 sp. *H. grypus*, the grey-seal of the British Isles, attains to 8 feet in length, Atlantic. *Phoca* L., 6 species, N. Hemisphere; *P. vitulina*, the common seal, British Isles, 4 to 5 feet in length, ascends rivers, Arctic Ocean, N. Atlantic and Pacific; *P. caspica*, Caspian and Aral Seas; *P. sibirica*, Lake Baikal; *P. groenlandica*.

Sub-fam. 2. **Monachinae.**  $i \frac{3}{2}$ , the outer digits of the pes exceed the others in length, with small or absent nails. *Monachus* Flem., 1 sp. *M. albiventer*, monk-seal of the Mediterranean and Atlantic. *Ogmorhinus* Pet., 1 sp. *O. leptonyx*, the sea-leopard, Antarctic and southern temperate seas; *Lobodon* Gray, 1 sp., Antarctic Ocean. *Leptonychotes* Gill., 1 sp., Ant. Ocean; *Ommatophoca* Gray, 1 sp., Ant. Ocean.

Sub-fam. 3. **Cystophorinae.**  $i \frac{2}{1}$ , outer digits of pes longer than the others, nails small or absent. *Cystophora* Nils., 1 sp. *C. cristata*, hooded or bladder-nosed seal of the N. Atlantic, occasionally visits the British coasts; with a dilatable sac upon the face. *Macrorhinus* F. Cuv., the elephant seal; nose produced into a short proboscis capable of dilatation, 1 sp., *M. leoninus*, the sea-elephant, attaining a length of nearly 20 feet, Antarctic Ocean and N. Pacific (California).

## Order 18. RODENTIA\* (GLIRES).

Usually plantigrade animals with a pair of large sharp chisel-shaped rootless incisors in each jaw and without canines. The grinding teeth are either lophodont or bunodont; the articular surface for the lower jaw is nearly always longitudinally elon-

\* Waterhouse, *Natural History of the Mammalia*, vol. 2, 1843. Brandt, Die craniologischen Entwicklungsstufen u. Class. der Nager der Jetzt



gated and the angular process of the jaw is well developed. There are never more than three papillae circumvallatae on the tongue.

The rodents are usually small animals, though in a few cases, e.g. the capybara, they may attain to some size. They have fur which is often fine, but in some it may be modified into spines on the back. The limbs are usually pentadactyle. They are plantigrade or semiplantigrade and the nails on the digits are usually claw-like, but in a few cases they have the form of hoofs.

The dentition is their most characteristic feature. Canines are always absent and the lower jaw has never more than one pair of incisors. The upper jaw also has only two incisors except in the Duplicidentata (hares, rabbits and pikas), in which there is a second pair of small incisors behind the large pair. There is always a wide diastema behind the incisors. The grinding teeth vary from  $\frac{2}{2}$  in the *Hydromys* to  $\frac{6}{5}$  in the rabbit. Three pairs of these are molars, the rest premolars. If there are only three pairs of grinders or less than three there are no premolars. In the majority the grinding teeth are four pairs,  $p \frac{1}{1} m \frac{3}{3}$ . The premolars usually displace milk molars. The milk dentition is varied. In some forms with three pairs (e.g. *Muridae*) or less than three pairs (*Hydromys*) of grinders, there appear to be no milk teeth at all, and the dentition is monophyodont. In some forms (e.g. *Cavia*) milk grinders are present in the embryo, but absorbed before birth; in some (e.g. *Castor*) the milk grinders persist until the animal is half-grown; and there are conditions intermediate between these two. Milk incisors seem generally to be absent. They have however been detected in a few forms; e.g. three pairs have been detected in the squirrel as vestiges, while in the rabbit there appear to be two pairs of deciduous incisors in the upper jaw, and one pair in the

welt, *Mém. Acad. Imp. Petersbourg*, 1855. Forsyth Major, Nagerüberreste aus Süddeutschland u. der Schweiz, *Palaeontographica*, 22, 1873, p. 75. Alston, Class. of the order Glires, *P.Z.S.*, 1876, p. 61. Cowes and Allen, Monograph of N. American Rodentia, *U. S. Geol. Surv. Territ.*, 11, 1877. Schlosser, Die Nager der Europ. Tert., *Palaeontographica*, 31, 1884-5. Winge, Rodentia fra Lagos Santa, Brazil, *Mus. Lund.* 3, 1887. Thomas, Genera of Rodents, *P.Z.S.*, 1896, p. 1012. Tullberg, Das System d. Nagerthiere, *Act. Ak. Upsala*, 1899.

lower jaw. Of the former the anterior pair does not appear above the gum and is absorbed before birth, while the posterior is shed in the third week after birth; the milk incisors of the lower jaw are absorbed before birth. The large incisors appear always to be rootless and to grow throughout life. They extend far back into the jaws and are much curved. They have enamel only on their anterior faces except in the *Duplicidentata*, in which it extends on to their inner sides. The small incisors of the latter are also rootless and have enamel on both faces. By continuous wear they are kept to a sharp edge of enamel. In many rodents the enamel of the incisors is stained a yellow colour. The milk molars have roots, and are brachyodont. The permanent grinders are either brachyodont and rooted, or hypsodont and rootless, growing throughout life. In the latter case they are curved as in *Toxodon*, so as to take the pressure off the growing pulp. There is considerable variety in the surface of the crown according to the food (vide Tullberg, *op. cit.*). In omnivorous forms they are brachyodont and bunodont, the enamel of the crown not being much folded and wearing through with use, so that the surface comes to consist of dentine surrounded by an enamel ring. In the herbivorous forms, however, in which the wear is greater, they are hypsodont and continue to grow throughout life or through part of life, and the enamel is deeply folded into transverse ridges, the valleys between which may be filled in with cement. As a rule there are two or three ridges, but in the capybara, the last of the four grinders has a great number of these transverse enamel folds and appears to consist of many laminae embedded in cement. In these cases of lophodont molars the unworn tooth is tuberculated, the laminated pattern becoming apparent when the tubercles are worn off. The enamel varies in the arrangement of the prisms in different families, and in some cases dentinal tubes extend into it.

The long axis of the articular condyle of the lower jaw is directed longitudinally and the squamosal has no postglenoid process. There is a large tympanic bulla, and the tympanic is generally prolonged into a tubular meatus; it often remains distinct from the squamosal and periotic. The paroccipital processes of the exoccipital are long. The jugal occupies the

middle of the zygomatic arch, but is occasionally prolonged back to the glenoid cavity. The orbit is not closed behind and the frontal is without postorbital processes except in a few genera. The lacrymal foramen is intraorbital, and the infraorbital foramen is often very large, sometimes as large as the orbit (Hystricidae, etc.), transmitting part of the masseter muscle.

The nasals extend far forward and the premaxillae are large. There is usually an interparietal bone. The palate is narrow and the anterior palatal foramina extensive. The angular part of the mandible is considerable and the coronoid process low.

The dorsolumbar vertebrae are usually nineteen.

Clavicles are usually well developed but they may be feeble or absent. The scapula is narrow, and has an acromion usually with a metaacromion. The humerus is without an entepicondylar foramen, and the femur often has a third trochanter. The radius and ulna are distinct and sometimes capable of rotation, but the tibia and fibula are often united. The carpus has a centrale and the scaphoid and lunar are generally fused.

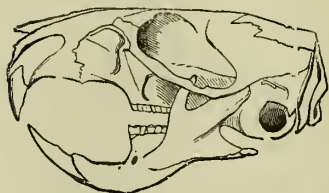


FIG. 325.—Skull of *Cricetus vulgaris* (from Claus).

There are usually five digits in the manus but the pollex may be reduced or absent. In the pes the digits vary from five to three and in the *Dipodidae* the metatarsals are much elongated and may be ankylosed.

The brain is small and the cerebellum is left uncovered by the cerebrum, the surface of which is usually but slightly convoluted. In the larger forms the convolutions are better developed and in the smaller they are absent, the surface being quite smooth.

The hairy integument of the face is often prolonged into the mouth behind the incisors, and there is thus a kind of antechamber to the mouth in which gnawed matter not intended for food may be intercepted. The hairy lining may extend even into the cheek pouches if these are present. In the *Geomyidae* the cheek pouches open externally on the

cheeks. The stomach is generally simple, but there may be complications. It may be constricted between the cardiac and pyloric portions with a groove leading from the oesophagus to the pyloric end and occasionally (e.g. *Castor*) there are cardiac glands. In *Myoxus* the oesophagus has a glandular dilatation at its lower end. There is always a large caecum except in *Myoxus* and the gall bladder is generally present. The colon is occasionally spirally twisted. There are two superior venae cavae. In some genera the ureters open into the fundus of the bladder. Vesiculae seminales are present except in the Duplicidentata and the penis usually has a bone. The testes are in most cases abdominal, descending into the inguinal region in the breeding season. In the Duplicidentata they may be said to descend into a scrotum in which they remain permanently. A prostate is present. The uterus is bicornuate, or may be quite double. They usually produce numerous young at a birth and have a considerable number of thoracic and abdominal mammae. The young are born naked and helpless in the burrowing forms. The placenta and the chorion are both discoidal.

Odoriferous glands are very generally present ; they open into the prepuce or into the rectum or near the anus.

The Rodentia are the largest mammalian order. There are about 1,400 species and 160 genera. They are cosmopolitan. They are most numerous in South America, which has been termed their home, and least so in Australia and Madagascar, where they are represented by only a few genera of Muridae.

They present great diversity of life. They all gnaw and are herbivorous. A few are omnivorous. It is possible that one or two may be carnivorous. Some are arboreal, and in the flying squirrels provided with a parachute-like membrane for floating in the air. Others are aquatic, as the water-vole, while yet others live on the earth and are strong runners, as the hares. Many of them build nests, dig out complicated burrows, and lay up stores for the winter. The latter usually possess cheek pouches. Some fall into a winter sleep at the cold season of the year.

Typical rodents are first found fossil in the Upper or possibly in the Lower Eocene, most of the remains belonging



to existing families and genera, and they seem to have undergone but little change since that period. There is no suggestion as to their origin, but similarities have been pointed out between them and the Proboscidea and Typotheria, the latter resembling them in their jaws, teeth, nasal bones and paroccipital processes of the skull.

### Sub-order 1. SIMPLICIDENTATA.

With one pair of upper incisors, without vesiculæ seminales, testes abdominal, descending into a temporary scrotum. The fibula does not articulate with the calcaneum.

#### Tribe 1. Sciuromorpha.

Skull with slender zygomatic arch, clavicles well developed, fibula free, infraorbital foramen small except in Anomaluridae.

Fam. 1. **Anomaluridae**. Arboreal forms, with their limbs connected by a patagium, supported by a cartilaginous fascia arising from the olecranon; tail long, hairy, with large scales on its ventral surface near the root;  $p \frac{1}{4}$ ; molars with transverse enamel loops; Ethiopian. *Anomalurus* Wat., 9 sp. *Idiurus* Matsch., 1 sp. *Zenkerella* Matsch., 1 sp.

Fam. 2. **Sciuridae**. Squirrels. Arboreal or terrestrial, with cylindrical hairy tails, often brilliantly coloured; skull with postorbital processes,  $p \frac{2}{3}$ , molars rooted, tubercular; cosmopolitan, excluding Australasian region and Madagascar. *Rheithrosciurus* Gray, 1 sp., Borneo, with grooved incisors. *Xerus* H. and E., spiny squirrels, Afr. (Ethiopian and Palaearctic), 5 sp., terrestrial, burrowers. *Sciurus* L., cosmopol., except Austr. and Madgr., 106 sp.; manus 4 digits and reduced pollex, pes 5 digits, first upper p. minute, soon lost; no cheek pouches; *S. vulgaris*, common English squirrel, ranges to Japan. *Tamias* Ill., ground squirrels, chipmunk, Nearctic, 30 sp., Palaearctic, 1 sp., with cheek pouches. *Spermophilus* F. Cuv., pouched marmots, sousliks, burrowers, Nearct., Palaearct., 40 sp. *Cynomys* Raf., prairie dogs, burrowers, live in communities, often with a burrowing owl and a rattlesnake, Nearct., 4 sp. *Arctomys* Schr., marmots, burrowers, Nearct., Palaearct., 10 sp.; *A. marmotta*, the alpine marmot. *Eupetaurus* Thos., flying squirrel, Oriental, 1 sp., patagium as in the next, with hypsodont grinders. *Petaurista* Link. (*Pteromys* G. Cuv.), flying squirrels, Oriental, 13 sp., limbs united by an expansion, the support of which articulates with the carpus. *Sciuropterus* F. Cuv., flying squirrels, Oriental 17 sp., Nearct. 5 sp., Palaearct. 2 sp., patagium as in the last. *Nannosciurus* Trouess., Ethiop. 1 sp., Oriental 2 sp. Extinct genera from the U. Eocene onwards.

Fam. 3. **Castoridae**. Beavers,  $p \frac{1}{4}$ , molars rootless, without postorbital process, stomach with a large glandular appendage, anus and urinogenital duct open into a common cloaca, pes webbed. *Castor* L., burrowers on the banks of rivers, 2 sp.; *C. fiber*, European, formerly British, do not as a rule make dams; *C. canadensis*, N. Amer., construct dams. Extinct sp. and genera from the Miocene onwards.

Fam. 4. **Haplodontidae**. *Haplodon* (*Aplodontia*) Rich., 2 sp., Nearct.

Tribe 2. **Myomorpha.**

Skull with slender zygomatic arch, clavicles well-developed, except in *Lophiomys*, tibia and fibula united, infraorbital foramen variable.

Fam. 5. **Gliridae** (*Myoxidae*). Dormice, small, arboreal, with long hairy tails, intestine without caecum,  $p \frac{1}{4}$ , molars rooted, lophodont. Palearctic, Ethiopian, Oriental. *Glis* Briss. (*Myoxus*), Palearctic, 1 sp. *Muscardinus* Kaup., Palearct., 1 sp. *M. avellanarius*, common dormouse, Brit. and Eur. *Eliomys* Wagn., Palearct., 2 sp. *Graphiurus* F. Cuv. Ethiopian, 13 sp. *Platacanthomys* Blg., Oriental, 1 sp. *Typhlomys* M. Edw., Oriental, 1 sp.

Fam. 6. **Muridae**. Rats, mice, Australian water rat, hamster, etc. Without premolars; molars rooted or rootless, bunodont or lophodont; frontals contracted; pollex reduced, often with a small nail; tail rarely densely-haired, sometimes scaly. There are about 86 genera and 724 species. Cosmopolitan, being found in Australasia (*Hydromys*, *Xeromys*, *Mus*, *Pogonomys*, *Craurothrix*, *Mastacomys*, *Uromys*, *Conilurus*), and in Madagascar (*Brachytarsomys*, *Nesomys*, *Hallomys*, *Brachyuromys*, *Hypogeomys*, *Gymnuromys*, *Eliurus*). The following may be mentioned: *Hydromys* Geoff., Australian water-rats, molars  $\frac{2}{3}$ , Australia, Tasmania, N. Guinea, 4 sp. *Xeromys* Thos.,  $m \frac{2}{3}$  Queensland, 1 sp. *Celaenomys* Thos., *Chrotomys* Thos., *Crunomys*, *Rhynchomys* Thos., *Phlaeomys* Wat., all Oriental with 1 sp. *Gerbillus* Desm., Ethiop. 20 sp., Orient. 2 sp., Palearct. 16 sp., burrowers, with tufted tails, jerboa-like. *Mus* L., rats and mice, largest genus of mammals, Aust. 30 sp., Eth. 30 sp., Orient. 50 sp., Palearct. 20 sp., absent from the New World, 5 British species. *M. minutus*, harvest mouse,  $2\frac{1}{2}$  in.; *M. sylvaticus*, wood-mouse; longer ears than *M. musculus*, the common house mouse, probably a native of Asia; *M. rattus*, the black rat; *M. decumanus*, the Hanoverian rat or brown or Norway rat. *Lophiomys* M.-Edw., Eth., 1 sp., hallux, opposable, temporal fossa covered by a bony plate from the parietal to the jugal, as in turtles. *Cricetus* G. Cuv. (*Hamster*), hamsters, Palearct., 12 sp., with large cheek pouches, 8-9 inches, with short tails. *Microtus* Schrank (*Arvicola*), voles, Nearct. 40 sp., Palearct. 40 sp., short ears, short hairy tail, molars composed of triangular prisms placed alternately, 3 British species, *M. amphibius*, water-rat, feet not webbed; *M. agrestis*, field-vole, occasionally appearing in immense numbers and doing much damage; *M. glareolus*, bank-vole. *Lemmus* Link. (*Myodes* Pall.), lemming, Nearct. 1 sp., Palearct. 3 sp.; *L. lemmus*, the Scandinavian lemming, 5 inches, at indefinite intervals it multiplies excessively, and migrates in a straight line in enormous herds, crossing all obstacles till it reaches the sea into which it plunges in the continuance of its wandering and is drowned; during the migration, which may last 1-3 years, it continues to multiply abnormally and is attacked by all animals en route and destroyed in large numbers; many perish from disease, due to over-crowding, none appear to return; the instinct is a good instance of a useless character. *Siphneus* Bts., Palearct., 5 sp., mole-like, subterranean creatures. *Fiber* G. Cuv., musk-rat, musquash, Nearct., 3 sp., *F. osoyoocensis*, builds nests on bulrushes above water, carnivorous. *Pachyuromys*, Ethiop. 1 sp., Palearct. 1 sp. *Meriones*, *gerbil* or Ethiop. 2 sp., Orient. 1 sp., Palearct. 10 sp. *Psammomys*, Palearct., 2 sp. *Rhombomys*, Palearct., 1 sp. *Otomys*, Eth., 4 sp. *Oreinomys*,

*gerbil*

Eth., 1 sp. *Deomys*, Eth., 1 sp. *Dendromys*, Eth., 6 sp. *Limacomys*, Eth., 1 sp. *Steatomys*, Eth., 4 sp. *Malacothrix*, Eth., 1 sp. *Nesokia*,<sup>\*</sup> Orient. 8 sp., Palaearct., 4 sp. *Cricetomys*, Eth., 1 sp. *Malacomys*, Eth., 3 sp. *Lophuromys*, Eth., 4 sp. *Saccostomus*, Eth., 3 sp. *Acomys*, Eth., 7 sp., Palaearct. 3 sp. *Arvicanthis*, Eth. 9 sp., Palaearct. 2 sp. *Dasymys*, Eth., 4 sp. *Golunda*, Eth. 2 sp., Orient. 1 sp. *Vandeleuria*, Orient., 1 sp. *Chiropodomys*, Orient., 3 sp. *Batomys*, Orient., 1 sp. *Carpomys*, Orient., 2 sp. *Pogonomys*, Aust., 8 sp. *Hapalomys*, Orient., 1 sp. *Pithecocheirus*, Orient., 1 sp. *Lenomys*, Orient., 1 sp. *Crateromys*, Orient., 1 sp. *Malomys*, Orient., 1 sp. *Craurothrix*, Aust., 1 sp. *Mastacomys*, Aust., 1 sp. *Uromys*, Aust., 8 sp. *Conilurus*, Aust., 16 sp. *Megalomys*, Neotrop., 1 sp. *Sigmodon*, Nearct., 7 sp. *Oryzomys* Neotrop. 60 sp., Nearct. 6 sp. *Chilomys*, Neotrop., 1 sp. *Reithrodontomys*, Neotrop. 3 sp., Nearct. 9 sp. *Eligmodontia*, Neotrop. 6 sp. *Nectomys*, Neotrop., 7 sp. *Neotomys*, Neotrop., 1 sp. *Reithrodon*, Neotrop., 5 sp. *Phyllotis*, Neotrop., 5 sp. *Scapteromys*, Neotrop., 2 sp. *Ichthyomys*, Neotrop., 4 sp. *Akodon*, Neotrop., 40 sp. *Mystromys*, Eth., 1 sp. *Brachytarsomys* Madagascar, 1 sp. *Nesomys*, Madagascar, 1 sp. *Hallomys*, Madagascar, 1 sp. *Brachyuromys*, Madagascar, 2 sp. *Hypogeomys*, Madagascar, 1 sp. *Gymnuromys*, Madagascar, 1 sp. *Eliurus*, Madagascar, 4 sp. *Onychomys*, Nearct., 8 sp. *Peromyscus*, Nearct., 30 sp. *Rhipidomys*, Neotrop., 12 sp. *Tylomys*, Neotrop., 3 sp. *Holochilus*, Neotrop., 4 sp. *Oxymycterus*, Neotrop., 8 sp. *Blarinomys*, Neotrop., 1 sp. *Notiomys*, Neotrop., 1 sp. *Neotoma*, Neotrop. 1 sp., Nearct. 33 sp. *Nelsonia*, Nearct., 1 sp. *Xenomys*, Nearct., 1 sp. *Hodomys*, Nearct., 1 sp. *Phenacomys*, Nearct., 6 sp. *Erotomys*, Nearct. 14 sp. Palaearct. 5 sp. *Synaptomys*, Nearct., 7 sp. *Dicrostonyx*, Nearct. 1 sp., Palaearct. 1 sp. *Ellobius*, Palaearct., 4 sp.

Fam. 7. **Spalacidae**. Mole-like forms, with very small sometimes vestigial eyes and pinna, and short tail; molars rooted, lophodont. *Spalax* Güld., Palaearct., 8 sp. *Rhizomys* Gray, bamboo-rats, Orient., 5 sp. *Tachyoryctes* Rupp. Ethiop., 3 sp.

Fam. 8. **Geomyidae**. Pouched rats. Fossorial with large cheek pouches opening on the cheeks outside the mouth, *p*  $\frac{1}{2}$ . *Geomys* Raf., pocket-gopher, Nearct., 8 sp. *Thomomys* Max., Nearct., 1 sp.

Fam. 9. **Heteromyidae**. Burrowing, with long hind limbs and tail; all confined to Nearctic except *Heteromys*. *Dipodomys* Gray, kangaroo-rat, jerboa-like, with 4 or 5 toes on pes, 12 sp. *Perodipus* Fitz., 10 sp. *Microdipodops* Murr., 1 sp. *Perognathus* Wied., 38 sp. *Heteromys* Desm., Nearct. 12 sp., Eth. 3 sp.

Fam. 10. **Bathyergidae**. Subterranean, mole-like, with small eyes and pinna, short legs and tail, hairs reduced, the upper incisors stand out in front of the closed lips, premolars present or absent, all Ethiopian. *Bathyergus* Ill., Cape mole-rat, 1 sp. *Georchus* Ill., 10 sp. *Myoscalops* Thos., 3 sp. *Heterocephalus* Rüpp., 2 sp., Somaliland, with nearly naked skin.

Fam. 11. **Dipodidae**. Jerboas, terrestrial usually with 4 u. grinders, rooted, lophodont; infraorbital foramen large; metatarsals greatly elongated, often fused into a cannon bone, pes from 3 to 5 digits, all Palaearctic except *Zapus*. *Sminthus* Keys. and Blas., 4 sp. *Zapus* Coues, Nearct. 6 sp., Palaearct. 1 sp. *Dipus* Gmel., 10 sp., pes 3-toed, metatarsals ankylosed, cervical vertebrae except atlas ankylosed; leap and burrow. *Atacaga* F. Cuv., 10 sp. *Platycomys* Brandt., 1 sp. *Euchoreutes* W. Schl. 1 sp.

*Nesokia* is now split into two gener., one comprising  
Bandicoots, the other mole-rats.

Tribe 3. **Hystricomorpha.**

With stout zygomatic arch, clavicles perfect or imperfect, fibula distinct, infraorbital foramen large,  $p \frac{1}{2}$ .

Fam. 12. **Pedetidae.** With rooted molars, cervical vertebrae free, hind limbs elongate, metatarsals free, pes tetradactyle, Ethiopian. *Pedetes* Ill., 1 sp.; *P. kaffer*, the Cape jumping-hare.

Fam. 13. **Octodontidae.** Clavicles complete, grinders with external and internal enamel folds, anterior palatal foramina long extending into maxillae, manus and pes usually with 5 digits, teats high up on the flanks, tail with short hairs or scales, usually terrestrial, occasionally fossorial or aquatic, all Neotropical unless otherwise mentioned, 21 genera. *Loncheres* Ill., porcupine-rats, with small spines in the fur, 18 sp. *Thrynomys* Fitz. (*Aulacodus*), ground rat of S. Afr., 4 sp., Eth. *Myocastor* Kerr (*Myopotamus*), 1 sp.; *M. coypu*, the coypu, a large S. American water-rat, to 2 feet. *Ctenodactylus*, 1 sp., Eth. *Massoutiera*, 1 sp. Eth., 1 sp. Palaeart. *Pectinator*, 1 sp., Eth. *Petromys*, 1 sp., Eth. *Ctenomys*, 9 sp. *Aconaemys* (*Schizodon*), 1 sp. *Spalacopus*, 1 sp. *Octodon*, 4 sp. *Abrocoma*, 2 sp. *Dactylomys*, 1 sp. *Thrinacodus*, 1 sp. *Kannabateomys*, 1 sp. *Thrichomys*, 4 sp. *Cercomys*, 1 sp. *Carterodon*, 1 sp. *Mesomys* 4 sp. *Echinomys*, 13 sp. *Capromys*, 5 sp. *Plagiodontia*, 1 sp.

Fam. 14. **Hystriidae.** Porcupines. Fur more or less modified into spines and hollow quills, tail not prehensile, soles of feet smooth, grinding teeth with external and internal folds; skull bones often inflated by air-sinuses, clavicle incomplete, limbs sub-equal. *Hystrix* L., Ethiop. 3 sp., Orient. 7 sp., Palaeart. 2 sp.; *H. cristata*, the common porcupine, S. Eur., N. and W. Afr. *Atherura* G. Cuv., Ethiop. 3 sp., Oriental 1 sp. *Trichys* Gunth., Orient., 1 sp.

Fam. 15. **Erethizontidae.** Hair as in last, clavicles complete, soles tuberculated, tail usually prehensile, Neotropical except *Erethizon* F. Cuv., Nearctic, 2 sp.; *Coendu* Lac. (*Cercolabes* and *Synetheres*, *Sphingurus*), tree porcupines, arboreal, Neotrop. 9 sp. *Chaetomys* Gray, Neotrop., 1 sp.

Fam. 16. **Chinchillidae.** Terrestrial, with long hind limbs, bushy tails, soft fur, and complete clavicles, grinders lophodont, all Neotropical. *Chinchilla* Benn., 1 sp., squirrel-like, fur grey, valuable; Andes. *Lagidium* Mey., 3 sp. *Lagotomus* Brooks, 1 sp. *L. trichodactylus*, viscacha, live in burrows.

Fam. 17. **Dasyproctidae.** With long incisors, sub-equal limbs, hoofs like claws, short tail, Neotropical. *Dasyprocta* Ill., agoutis, pes with 3 digits, C. and S. Amer. and W. Ind. Islands, 12 sp.; *Coelogenys* F. Cuv., paca, pes with 5 digits, jugal arch very broad, enclosing on each side a cavity communicating with the mouth, body attains a length of 2 feet.

Fam. 18. **Dinomyidae.** Cleft upper lip, long bushy tail, limbs tetradactyle, 1 genus and sp. and only 1 specimen found, Peru. *Dinomys* Pet.

Fam. 19. **Caviidae.** Terrestrial or aquatic with short incisors, lophodont grinders, milk teeth shed in foetal life, paroccipital processes long and curved, clavicles imperfect, tail short, manus with 4, pes with 3 digits, Neotropical. *Cavia* Pall., caviés, 11 sp.; *C. porcellus*, guinea pig. *Dolichotis* Desm., 2 sp., Patagonian cavy. *Hydrochoerus* Briss., 1 sp., *H. capybara*, capybara, aquatic, the largest rodent, length 4 to 5 feet, without tail, manus tetra-, pes tri-dactyle, digits webbed, hoof-like nails, last u. molar very large with 14 laminae.



## Sub-order 2. DUPLICIDENTATA.

Incisors at birth  $\frac{6}{2}$ , the outer upper soon lost, the next pair small and placed behind the large third pair (p. 628). Skull with optic foramina confluent, without alisphenoid canal. Fibula ankylosed to tibia and articulating with calcaneum. Testes permanently external; without vesiculæ seminales.

Fam. 20. **Lagomyidae.** Picas,  $p \frac{1}{1}$  or  $\frac{2}{2}$ , grinders rootless lophodont, skull depressed, clavicles complete, ears short, no external tail. *Lagomys* G. Cuv. (*Ochotona* Link.), pica, tailless hare, mountainous parts of N. Asia, S. E. Eur. and Rocky Mountains, 16 sp.

Fam. 21. **Leporidae.** Hares and rabbits,  $p \frac{3}{2}$ , skull compressed, frontals with large wing-like postorbital processes, facial portion of maxillae reticulated, clavicles imperfect, ears and hind limbs long, tail short; cosmopolitan except Australasia and Madagascar. *Romerolagus* Merr., 1 sp., Neotrop. *Lepus* L., hares and rabbits; manus 5, pes 4 toes, about 20 sp. *L. timidus (europaeus)*, hare; *L. cuniculus*, rabbit, produces naked young and lives in burrows. The common hare, lives on its "form," produces active young, extends all over Europe, not known in Ireland. *L. variabilis*, the mountain hare, often changes colour in winter, but does not change in Ireland.

## Order 19. INSECTIVORA.\*

*Terrestrial, rarely arboreal or natatorial mammals of small size, with plantigrade or semiplantigrade, generally pentadactyle, unguiculate feet; with clavicles (except in Potamogale); with more than two incisors in the mandible, and with enamelled, tuberculated rooted molars.*

The Insectivora are small animals covered with fur and sometimes on the dorsal and lateral surfaces with spines. The limbs are usually pentadactyle, and the digits are armed with claws. They are plantigrade or semi-plantigrade, and digit No. 1 is not opposable in either foot. The extremity of the muzzle projects beyond the end of the mandible.

The dentition contains all kinds of teeth, but in many cases the incisors, canines and premolars are not clearly differentiated from one another; it sometimes attains the full

\* Peters, Die Classification der Insectivoren, *Monatsb. Akad. Wissenschaft.* Berlin, 1865. Mivart, Osteology of Insectivora, *P.Z.S.*, 1871. Gill, Synopsis of Insectivorous Mammals, *Bull. Geol. and Geog. Survey, U.S.A.*, 1875. Dobson, *Monograph of the Insectivora*, London, 1882-90. Id., Synopsis of the Soricidae, *P.Z.S.*, 1890, p. 49, 1891, p. 349. Id., Insectivora in Blanford's *Fauna of British India*. Schlosser, *op. cit.*, see Carnivora.

mammalian number of teeth,  $i \frac{3}{3} c \frac{1}{1} p \frac{4}{4} m \frac{3}{3}$  (e.g., *Talpa*, *Myogale*), but there are usually reductions. The incisors are primitively conical, and are occasionally enlarged in a rodent-like manner. The posterior incisor sometimes has two roots (*Erinaceus*, *Galeopithecus*). The canines are not usually strongly developed and may have two roots (*Erinaceus*, *Talpa*, *Galeopithecus*). The premolars are usually sharp and pointed, but the last may be like the molars. The upper molars are three- or four-cusped, the cusps being isolated or connected by ridges. The last molar is frequently smaller than the others. The lower molars have three cusps in front and a talon which is often two-cusped behind. There is a milk dentition, which however is frequently absorbed in utero.

The skull is elongated and depressed, and has a small cranial cavity. The orbit is not closed by bone except in the Tupaiidae. The palate is very generally incompletely ossified, and the angle of the mandible may be inflected as in marsupials; and as in that order the alisphenoid contributes to the anterior wall of the tympanic cavity. The tympanic bulla is rarely completely ossified and frequently falls off in the dry skull. The mastoid process is often marked and sometimes joins the postglenoid process of the squamosal below the external auditory meatus. The jugal is often weak and sometimes absent, in which case the zygomatic arch is incomplete.

The vertebral column presents considerable variations, both in number and character of vertebrae, even in different species of the same genus. The lumbar region often presents intercentra.

The scapula has a well developed spine with an acromion and often a metacromion. A clavicle is present in all except *Potamogale*. The humerus usually has an entepicondylar foramen, and the radius and ulna are generally separate. The scaphoid and lunar are fused in some genera (e.g. *Galeopithecus*, *Tupaia*, *Erinaceus*, etc.), and there is usually a centrale in the carpus. The manus has typically five digits, but the pollex may be aborted. The femur often has a third trochanter. The fibula is usually united with the tibia, but in a few genera it is free. The digits of the pes are five, but the hallux may be absent. The pelvis presents considerable variations; the pubic symphysis being long, short or absent (e.g. *Talpa*).

The brain is small. The cerebrum never projects back over

the cerebellum, and often leaves the optic lobes uncovered ; its surface is smooth, except for one shallow longitudinal sulcus on each side. The corpus callosum is small and the anterior commissure large. The stomach is simple (except in *Galeopithecus*). A caecum is present or absent. There are two superior venae cavae.

The testes are inguinal or abdominal and never descend into a scrotum. The penis is usually pendent, and in some forms is retractile within the fold of integument surrounding the anus. The uterus is bicornuate, and often without a distinct *os uteri*, the placenta discoidal, and the mammae which are generally numerous are variable in position. They frequently extend along the ventral surface from the axilla to the inguinal region, but occasionally they are axillary (*Galeopithecus*) or even post-inguinal (*Solenodon*). Odoriferous glands are present in many species. They may be just behind the axilla, as in the shrews, or near the anus.

The Insectivora are, with the exception of the Tupaiidae, nocturnal animals. Most of them are cursorial, but a few are burrowers (the moles), and some are aquatic (*Potamogale*, *Myogale*). Others again are arboreal (Tupaiidae) and *Galeopithecus* flits about from tree to tree by means of a patagium as do the flying squirrels. They live on insects and worms.

They are generally regarded as the most primitive of placental mammals, and perhaps their nearest allies are the polyprotodont marsupials. In their dentition and in the structure of the skull and brain they recall the Chiroptera, and by their fossil forms they approximate to the Creodonta and Lemuroidea.

The primitive characters are the small and smooth brain, the frequent occurrence of trituberculate molars, the absence of a scrotum, and the frequent abdominal position of the testes ; moreover the palate is often fenestrated and the angle of the mandible inflected, and sometimes the anus and urinogenital apertures are surrounded by a common fold of integument, so that there is a kind of cloaca.

They are widely distributed over the earth's surface, but are entirely absent from the Australian region, and in South America are only found in the northern Andes.

They make their appearance in the Lower Eocene of Europe and North America. Many of the older forms are not referable

to existing families and present greater resemblance to marsupials, creodonts and lemuroids than do the more modern types.

Fam. 1. **Tupaïidae**. Arboreal diurnal forms with large brain case, closed orbit and well-developed zygomatic arch, perforated jugal, a tympanic bulla, and a long symphysis pubis. Upper molars broad, multi-cuspidate, with cusps arranged in a W; usually with a short caecum; Oriental region. *Tupaia* Raffles, tree-shrews,  $i \frac{2}{3} c \frac{1}{1} p \frac{3}{3} m \frac{5}{3}$ , about 14 species, squirrel-like. *Ptilocercus* Gray, pen-tailed tree-shrew, 1 sp., Borneo. Extinct genera from the M. Miocene; *Lantanoherium*, *Plesiosorex*, *Gularix*.

Fam. 2. **Macroscelididae**. Nocturnal saltatorial forms with large brain case, well-developed zygomatic arch, imperforate jugal, orbit not surrounded by bone, a tympanic bulla and a long symphysis pubis. The metatarsus is greatly elongated, the tibia and fibula are united, and the caecum is large. The penis is anterior and suspended from the abdominal wall. The molars are broad and have four cusps arranged in a W. Africa. *Macroscelides* A. Smith, jumping or elephant-shrews, 10 sp.; *Petrodromus* Pet., 3 sp.; *Rhynchocyon* Pet., fossorial, 4 sp.

Fam. 3. **Erinaceidae**. Hedgehogs. Terrestrial forms with plantigrade feet, small brain case, slender zygomatic arch, an annular tympanic not forming a bulla; without postorbital process; with slender clavicles and bifid acromion; radius and ulna free, tibia and fibula ankylosed; caecum absent. The spinal chord is much thickened in the cervical region and is continued as a slender filament, the *filum terminale*. The penis is anterior and suspended from the abdominal wall.  $m$  1 and 2 of upper jaw with 5 cusps, the central cusp being minute and united by a ridge on each side to the two internal cusps; Palaearctic, Ethiopian (except Madagascar), and Oriental regions. *Gymnura* Horsf. and Vig.,  $i \frac{3}{3} c \frac{1}{1} p \frac{4}{4} m \frac{3}{3}$ , without spines, Malayasia. *Erinaceus*, L hedgehogs;  $i \frac{3}{2} c \frac{1}{1} p \frac{3}{2} m \frac{3}{3}$ , with spines; about 20 species, Palaearctic, Ethiopian and Oriental regions; *E. europaeus* L., the common hedgehog, hibernates during the winter, young born in July or August. Extinct genera from the Miocene and Eocene.

Fam. 4. **Soricidae**. Shrews. Terrestrial, rarely aquatic, rat-like or mouse-like forms, with long and pointed muzzle; without zygomatic arch, postorbital process, and pubic symphysis; the tympanic is annular, the tibia and fibula are united, and the cusps of the u. molars are arranged in a W; widely distributed. The dentition is not fully understood, owing to the early obliteration of the maxillo-premaxillary suture. The ordinary statement is that there are four incisors, one canine, a variable number of premolars and three molars in the upper jaw, but it is possible that the fourth incisor may be the canine, and the canine the first premolar. There are always three molars. In the lower jaw there are always six teeth (possibly seven in *Myosorex*) on each side. There is no caecum or symphysis pubis, and the penis is retractile within the fold of the integument surrounding the anus. This family includes the majority of species of the order.

Sub-fam. 1. **Soricinae**. Teeth tipped with red. *Sorex* L.,  $i \frac{4}{2} c \frac{1}{1} p \frac{2}{2} m \frac{3}{3}$ , milk dentition functionless; terrestrial; urogenital opening separated from the anus, ears well-developed, tail long; Palaearctic and Nearctic; two British species, *S. vulgaris*,



the common shrew, and *S. minutus*, which is rarer; in the former there is a gland opening on each side of the body and emitting an odoriferous fluid. *Soriculus* Blyth, Oriental. *Notiosorex* Coues, C. Amer., Mexico. *Blarina* Gray, N. American short-tailed shrew. *Crossopus* Wag.,  $i \frac{3}{2}$   $c \frac{1}{0}$   $p \frac{2}{1}$   $m \frac{3}{3}$ , urinogenital opening and anus enclosed in a common ring, ears small, tail long, aquatic; *C. fodiens*, the water-shrew, of Britain (not Ireland), Europe, Asia; is considerably larger than the common shrew.

Sub-fam. 2. **Crocidurinae**. Teeth white. *Myosorex* Gray,  $i \frac{3}{2}$   $c \frac{1}{0}$   $p \frac{1}{1}$   $m \frac{3}{3}$ , terrestrial, Africa. *Crocidura* Wag., terrestrial, with cloaca, about 70 species, Eur., Afr., Asia. *Diplomesodon* Brandt, terrestrial, 1 sp., Asia. *Anurosorex* M.-Edw., mole-like, terrestrial, 2 sp., Asia. *Chimarrogale* Anderson, aquatic Asia, 2 sp. *Nectogale* M.-Edw., aquatic 1 sp., Thibet. Fossil forms as far back as the Eocene.

Fam. 5. **Talpidae**. Fossorial, rarely natatorial or cursorial forms, with fore-limbs generally modified for digging and anteriorly placed; humerus short, articulating with scapula and clavicle; tibia and fibula united; without symphysis pubis; with elongated skull, slender zygoma, and tympanic bulla; without postorbital process; without caecum;  $i \frac{3}{3 \text{ or } 1}$   $c \frac{1}{1 \text{ or } 0}$   $p \frac{1 \text{ to } 2}{1 \text{ or } 2}$   $m \frac{3}{3}$ ;  $i$ ,  $c$  and  $p$  vary much in form,  $m$  with W-shaped cusps. Eyes small and sometimes covered by the skin. Ears short and concealed by the fur. Penis pendent in front of the anus. Clitoris like the penis and traversed by urethra. The moles possess an elongated radial sesamoid (*os falciforme*), articulating with the scaphoid. Nearctic, Palaearctic, and N. parts of Oriental.

Sub-fam. 1. **Myogalinae**. Without *os falciforme*. *Myogale* Cuv., with webbed feet, aquatic, 2 sp., Eur., Asia. *M. moschata*, the desman, S.-E. Russia, 16 in. in length; *M. pyrenaica*, Pyrenees. *Urotrichus* Tem., mole-shrews, fossorial, Japan and N. Amer., 2 sp.

Sub-fam. **Talpinae**. Manus with *os falciforme*. *Scalops* Cuv., N. Amer., 3 sp. *Scapanus* Pomel., 3 sp., N. Amer. *Condylura* Ill., 1 sp., N. Amer. The above are New World moles. The following are Old World moles. *Scaptonyx* M.-Edw., 1 sp., Thibet. *Talpa* L., moles, usual dentition,  $i \frac{3}{3}$   $c \frac{1}{1}$   $p \frac{4}{4}$   $m \frac{3}{3}$ , 5 sp.; *T. europaea* the common mole, eye small, but uncovered, tail long and hairy; the sternum is keeled, the humerus and clavicle short and powerful, a very powerful burrower, voracious, hunting earthworms, Palaearctic.

Fam. 6. **Adapisoricidae**. Extinct, L. Eocene.

Fam. 7. **Potamogalidae**. Without clavicles, zygomatic arches, and postorbital processes; tympanic annular. The male and female organs and anus open within the same fold of integument, and the penis can be wholly retracted. Ethiopian. *Potamogale* Du Chaillu, a long animal, nearly 2 feet in length, inhabiting the banks of streams; W. Afr. *Geogale* M.-Edw., Madagascar.

Fam. 8. **Solenodontidae**. Without zygomatic arches and postorbital processes; tympanic annular. Penis pendent and anterior, testes received into perineal pouches; upper molars tritubercular; mammae two, placed on the buttocks; single genus. *Solenodon* Brandt, Cuba and Hayti.

Fam. 9. **Centetidae**. Without zygomatic arch and postorbital pro-

cesses; tympanic annular. Upper molars tritubercular. Penis pendent and retractile within the fold of integument surrounding the anus. In the female the urinogenital organs and anus open together. The testes are near the kidneys. Caecum absent. Madagascar. *Centetes* Ill., 1 sp. *C. ecaudatus*, the tenrec, 12–16 in. in length without a tail. *Hemicentetes* Miv. *Ericulus* I. Geoff. *Microgale* Thos. *Oryzoryctes* Grandidier.

Fam. 10. **Chrysochloridae.** Without postorbital process, with zygomatic arch and tympanic bulla, with stout fossorial fore-limbs, without symphysis pubis. The eyes are covered with skin and the ears without pinnae. Mammae thoracic and inguinal. Dentition  $i \frac{3}{3} c \frac{1}{1} p \frac{3}{3} m \frac{3 \text{ or } 2}{3 \text{ or } 2}$ , upper molars tritubercular. Generative organs as in Centetidae. S. Africa. *Chrysochloris* Lac., Cape golden moles, 7 or 8 sp.

Fam. 11. **Galeopithecidae.\*** The single genus, *Galeopithecus* Pall., of this family has been placed amongst the bats and amongst the primates. It is now, however, generally regarded as an aberrant insectivore.† The essential peculiarity of the genus is the possession of a parachute-like flying membrane, the *patagium*, which enables its purely arboreal possessor to float from tree to tree in the forests which it inhabits. The patagium is a muscular membrane, extending between the neck and the fore-limbs, between the fore- and hind-limbs, and between the hind-limbs and the tail. It is covered with hair on both sides, and, though it extends as a kind of web between the digits of both manus and pes, the fingers are not elongated, as they are in the bats, to support the anterior part of it. The dentition is  $i \frac{2}{3} c \frac{1}{1} p \frac{2}{2} m \frac{3}{3}$ ; the upper and lower incisors are compressed and multicuspidate, the lower pectinated, and the second upper incisor and the canines of both jaws have two roots. The orbit is nearly enclosed by bone, the posterior margin of the palate is thickened, the tympanic forms a bulla, and the postglenoid process of the squamosal unites with the mastoid beneath the external auditory meatus. The fore-limbs are slightly larger than the hind-limbs, and there are five clawed fingers and toes. There is a large sacculated caecum, and the large intestine is longer than the small. There are two pairs of axillary mammae, the penis is pendent, and the testes descend into inguinal pouches. The optic lobes are uncovered and the upper surface of the cerebrum is marked by two longitudinal furrows on each side. *Galeopithecus* differs entirely from the bats in the structure of the fore-limb, and in the position of the hind-limb. It resembles the insectivores in the structure of the skull, in the double-rooted canines (found also in *Erinaceus* and *Talpa*). There are two species, which inhabit the forests of Malayasia and the Philippine Islands. They are nocturnal, phytophagous animals, and when at rest hang by their posterior limbs with the head downwards, after the manner of bats.

## Order 20. CHIROPTERA.‡

*Flying mammals with the fore-limbs specially modified for flight.*  
*With one (or two) pairs of thoracic, usually postaxillary, mammae.*

\* Leche, Ueber *Galeopithecus*, K. *Svensk. Akad. Handl.*, 1886.

† It is sometimes placed in a special sub-order of the Insectivora, the *Dermoptera*, and opposed to the rest of the order which are termed *Insectivora vera*.

‡ G. E. Dobson, *Catalogue of the Chiroptera in the British Museum*, 1878. Id., *New accessions to the Chiroptera; Report of the British Association*.

Among the marsupials (*Petaurus*), the rodents (*Pteromys*) and the insectivores (*Galeopithecus*), there is a number of forms which are assisted in jumping by a kind of parachute, which consists of a cutaneous expansion, the *patagium*, stretched between the limbs on each side. The patagium is much more completely developed in the bats; in these animals it is continued over the extraordinarily elongated fingers of the hand, and in virtue of its great size and elasticity constitutes a true organ of flight. The tail, when present, is included in the patagium, but the thumb and the foot are separate from it (Fig. 326).

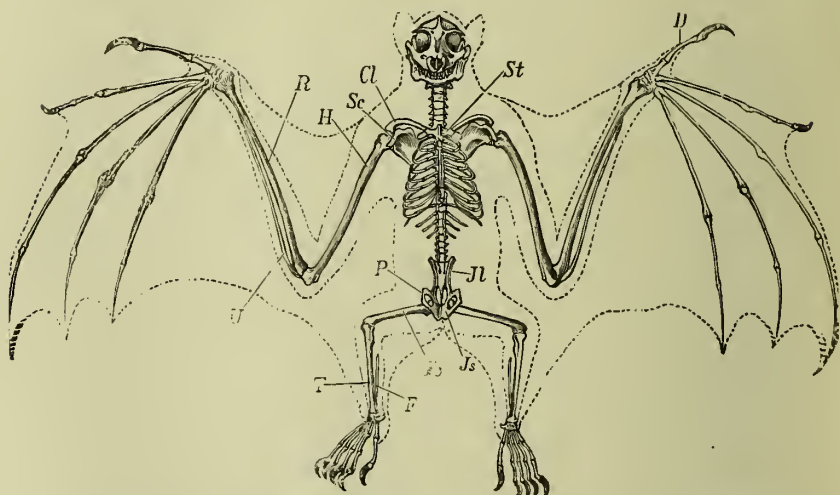


FIG. 326.—Skeleton of *Pteropus* (after Owen, slightly altered). *Cl* clavicle; *D* thumb; *F* fibula; *Fe* femur; *Il* ilium; *Js* ischium; *H* humerus; *P* pubis; *R* radius; *Sc* scapula; *St* sternum; *T* tibia; *U* ulna.

Both fore- and hind-limbs are pentadactyle. The thumb has two phalanges and is armed with a claw, as are also the five digits of the foot (Fig. 326). The second digit of the manus is also, in some forms, provided with a claw.

Peculiar outgrowths of the skin surrounding the nasal apertures (nose-leaf) are often present and give the face a very strange appearance (Fig. 327). Except upon these appendages and upon the thin elastic patagia, both of which have a large

*tion*, 1880. Allen, A Monograph of the Bats of North America, *Bull. U.S. Nat. Mus.*, No. 43, 1893. H. Winge, Chiroptera (viv. et foss.) ex Lagoa Santa, Minas Geraes, Brasil, *E. Museo Lundii*, 2, 1, 1892.

supply of nerves and a remarkably delicate sense of touch, the surface of the body is closely covered with hair.

The skeleton (Fig. 326) is remarkably light, and the bones of the limbs have large medullary cavities. It is distinguished by the large size and rigidity of the thoracic framework, by the possession of a keel on the presternum, by the length of the strongly developed sacrum with which the ischia are united, and by the fact that the anterior limbs are larger than the posterior, and possess four greatly elongated digits (digits 2-5). Moreover the hind-limb has been rotated outwards so that the knee is directed backwards and the sole of the foot forwards, the hallux being external. The calcaneum carries a bony or cartilaginous process, the *calcar*, which projects backwards and inwards supporting the interfemoral part of the patagium.

The cerebral hemispheres are smooth and do not extend over the cerebellum. The spinal cord is reduced to a fine thread in the lumbar-sacral region. The eyes are relatively small but the senses of hearing and of touch, and probably of smell, are enormously developed. Spallanzani has shown that bats which have been made blind are able to avoid all obstacles, such as strings stretched across a room, in their flight. The pinna of the ear is always large, and often of great size; it probably not only intensifies the power of hearing, but also acts as an organ of touch in the species in which the nose-leaf, which is probably the tactile organ *par excellence*, is not present.

The dentition never exceeds  $i \frac{2}{3} c \frac{1}{1} p \frac{3}{3} m \frac{3}{3}$ , and is frequently reduced from this. The alimentary canal is distinguished by the narrowness of the oesophagus, the relatively short length of the intestine and by the general absence of a caecum.

The heart and lungs are proportionately large. Both superior venae cavae are present.

In the reproductive system, the penis is pendent and often provided with a bone, the testes are abdominal, but descend into the perinaeum in the breeding season, and the clitoris is occasionally perforated by the urethra. The uterus may be rounded or bicornuate, and the placenta is discoidal and deciduate. They bear one or two young at a birth, and carry them about with them during their flight.

Bats are nocturnal animals. Some of them are insectivorous,



some frugivorous, and some (*Desmodus*, *Diphylla*) suck the blood of other mammals. When at rest they hang suspended by the claws of one or both legs, head downwards. On the ground they rest with the knees directed upwards, and move in a shuffling manner, pushing themselves along by their feet which are rotated forwards and inwards, and hauling themselves forwards by the claws on their thumbs. Many of them hibernate, and in some at least the sexual season is separated by a considerable interval from that of ovulation and conception (see p. 517). The sexes appear frequently to live apart except in the breeding season.

They are nearly cosmopolitan in distribution.\* There are about 520 species and 95 genera of living forms. The earliest fossil Chiroptera, which are from the Upper Eocene, show all the features of specialisation of the order. Remains of about 6 genera and 35 species have been discovered, all belonging to existing families.

Such are the principal characters of the Chiroptera. It is clear that they are a very sharply defined group with many peculiar features, and the diversity of structure within the group cannot be said to be very great. Formerly, on account of the usual number of their upper incisors, the position of the mammae, the pendent penis, the placental characters and the form of the uterus they were included amongst the Primates; but there can be very little doubt that their real affinities are with the Insectivora.

The following details may be added to the foregoing account.

The **nose-leaves** are found in the *Rhinolophidae*, the *Nycteridae* and the *Phyllostomidae*. They are folds of the skin at the margins of the nostrils, are richly supplied with nerves (mainly derived from the nasal branch of the trigeminal), and contain many sweat and sebaceous glands, which maintain their surfaces in a soft and highly sensitive condition. There can be no doubt that they are highly developed organs of touch, and are one of the principal means by which their possessors are able to feel objects without touching them, as bats are undoubtedly able to do. But this function must also be discharged by other organs; for the power of avoiding obstacles in the dark is, as was shown by Spallanzani's experiments, possessed by bats without a nose-leaf. These organs are probably the patagium, and the pinna of the ear which is remarkably developed in bats. The pinna is always large, and in some species its length

\* Dobson, *op. cit.*, states that they have not been found in Iceland, St. Helena, the Galapagos Archipelago, Kerguelen Island, and the Low Archipelago.

nearly equals that of the head and body. Its form is very diverse. In many species the *tragus* is greatly developed, and in the Rhinolophidae, in which the *tragus* is absent, compensation is probably afforded by the large *bullae osseae* and the largely developed nose-leaf.

The **patagium** consists of (1) the antebrachial portion which extends from the point of the shoulder along the humerus and more or less of the fore-arm to the base of the thumb, the metacarpal bone of which is partly or wholly included in it, (2) the wing-membrane which is spread out between the greatly elongated fingers, and extends along the sides of the body to the posterior limbs, generally reaching to the feet, and (3) the interfemoral membrane which is the most variable part and is supported between the extremity of the body, the legs and the calcar. In most species the wing-membrane arises from the sides of the body, but in a few (*Notopteris*, *Cephalotes*, etc.) it springs from the middle line of the back. The interfemoral membrane is best developed in the insectivorous forms, and aids them in their rapid doubling movements. In the frugivorous and blood-sucking species it is deeply cut out behind or forms a narrow projection along the legs.

Odoriferous glands and pouches opening on the surface of the skin are present in many species. The chief of them are the frontal pouches of *Phyllorhina*, the gular glands and pouches of *Taphozous*, *Molossus*, *Phyllostoma*, etc., the shoulder glands and pouches of *Pteropus*, etc., the pubic and anal glands of Rhinolophidae, etc., and the wing-pouches of *Saccopteryx*.

**Skeleton.** In addition to the points already noted, the following features may be mentioned. The vertebral column is short and constant in form. There are usually 12 thoracic and 5 lumbar vertebrae. With the exception of the axis none of the cervical or thoracic vertebrae develop spines. From the first thoracic to the last lumbar vertebra the spinal column forms a single curve backwards.

The skull is the most variable part of the skeleton. The postorbital processes of the frontal are absent or short in Microchiroptera, long and traversed by a foramen in Megachiroptera, and in *Pteropus leuopterus* the orbital ring is complete. The premaxillae are very variable, and may be cartilaginous or almost absent. The zygomatic arches may be strong, slender or absent. The tympanic bullae are without an external canal, and are loosely connected with the adjacent bones.

The clavicle is always well developed, and the spine of the scapula has a large acromion. The humerus has a large pectoral ridge, and is without a supracondylar foramen. The ulna is small and ankylosed with the radius. In the carpus the scaphoid, lunar and cuneiform are ankylosed to form a single bone and the distal bones are normal. The pollex always has a claw, as has the second digit in most Megachiroptera. The first, fourth and fifth digits possess two phalanges; in the second and third the number of phalanges varies. In Megachiroptera the second digit has three phalanges; in most Microchiroptera it only has a single rudimentary phalanx (absent in the Rhinolophidae). The third finger is the longest, and except in the Phyllostomidae and one or two others in which it has three, bears two phalanges only. The metacarpals and phalanges of the second to the fifth digits are for the most part elongated. The pelvic girdle is weak. The fibula is reduced except in the Molossinae.

**Dentition.** The molar teeth of the insectivorous forms are acutely tubercular, with usually well-developed W-shaped cusps. In the frugi-

vorous Megachiroptera the molar teeth are longer than broad and their crowns are traversed by a longitudinal groove. In the milk dentition the teeth have pointed recurved cusps which assist the young to secure a firm hold of the nipple of the mother during flight. They are shed early.

### Tribe 1. MEGACHIROPTERA.

Frugivorous bats, generally of large size. Crowns of the molar teeth smooth, marked with a longitudinal furrow; bony palate continued behind the last molar, narrowing slowly backwards; second finger generally terminating in a claw; sides of the pinna forming a complete ring at the base; pyloric extremity of the stomach elongated. The tail is short or absent, when present it is partly in the interfemoral membrane, except in *Epomophorus*, in which it is free from this structure. Tropical and sub-tropical regions of the Old World.

Fam. **Pteropidae**. With the characters of the tribe. *Epomophorus* Bennett, 10 sp., Ethiopian except Madagascar. *Pteropus* Briss., flying foxes, the largest known bats, with long pointed muzzle, without tail,  $i \frac{2}{2} c \frac{1}{1} p \frac{3}{3} m \frac{2}{3}$ , about 50 sp., Madagascar and Mascarene Islands, Oriental region, S. Japan, Australia and Polynesia (except Sandwich Islands, Ellice's group, Gilbert's group, Tokelau, Low Arch., and N. Zealand); *P. edulis* measures 5 feet across on the wing with a body-length of 12 inches. *Pteralopex* Thos., 1 sp., Solomon Islands. *Cynonycteris* Ptrs., 10 sp., Ethiop. and Orient. *Boneia* Jent., 2 sp., Malay Arch. *Harpyonictoris* Thos., 1 sp., Philippines. *Cynopterus* F. Cuv., 11 sp., Oriental. *Scotonycteris* Matschie, 1 sp., Cameroons. *Harpyia* Ill., with external nostrils prolonged as tubes,  $i \frac{1}{0} c \frac{1}{1} p \frac{2}{3} m \frac{2}{2}$ , 2 sp., Austro-Malaya. *Cephalotes* E. Geoff., 2 sp., Austro-Malaya. *Hypsignathus* Allen, 1 sp., Afr. *Leiponyx* Jent., 1 sp., Afr. *Eonycteris* Dob., 1 sp., Burmah. *Megaloglossus* Pag., 1 sp., Afr. *Macroglossus* F. Cuv., 3 sp., Oriental and Polynesia. *Melonycteris* Dob., 1 sp., New Ireland. *Callinycteris* Jent., 1 sp., Celebes. *Nesonycteris* Thos., 1 sp., Solomon Is. *Notopteris* Gray, 1 sp., Fiji, New Guinea.

### Tribe 2. MICROCHIROPTERA.

Mainly insectivorous bats of small size. Crowns of the molar teeth acutely tubercular, marked by transverse furrows; bony palate narrowing abruptly, not continued laterally behind the last molar; second finger not terminated by a claw and usually with one small phalanx only; outer and inner sides of the pinna commencing anteriorly from separate points of origin; stomach simple or with the cardiac extremity more or less elongated. Tropical and temperate regions of both hemispheres.

Fam. **Rhinolophidae**. With well developed foliaceous cutaneous appendages surrounding the nasal apertures, which are placed in a depression on the upper surface of the muzzle; with large, generally separated ears, without a tragus; first finger without phalanx, middle finger with two phalanges; with rudimentary premaxillae suspended from the nasal cartilages.  $i \frac{1}{2} c \frac{1}{1} p \frac{2}{3} m \frac{2}{3}$ ; the upper incisors are rudimentary, the molars have acute W-shaped cusps. They possess complicated nasal appendages, supported by the nasal bones which are much expanded. Females with 2 nipple-shaped appendages in front of the pubis. Tail distinct, reaching to the posterior margin of the interfemoral membrane.

They are the most highly organised of insectivorous bats. Temperate and tropical parts of the Old World (not found in Polynesia). *Rhinolophus* E. Geoffr., with complicated nose-leaf, and ear with large anti-tragus, wings large,  $i \frac{1}{2} c \frac{1}{1} p \frac{2}{3} m \frac{3}{3}$ ; more than 20 sp. *R. hipposiderus*, the lesser horseshoe bat, Eur., South of England and Ireland; *R. ferrum-equinum*, the greater horse-shoe bat, England to Japan and Cape of Good Hope. *Triaenops* Dob., with very remarkable nasal appendage and ears, Persia, Afr., Madagascar, 3 sp. *Rhinonycteris* Gray, 1 sp., Australia. *Phyllorhina* Bonap. 1831 (*Hipposiderus* Gray, 1834),  $i \frac{1}{2} c \frac{1}{1} p \frac{2}{2} m \frac{3}{3}$ , 25 sp., trop. and sub-trop. parts of Asia, Malayasia, Australia and Afr. *Anthops* Thos., 1 sp., Solomon Is. *Coelops* Blyth, 1 sp., India.

**Fam. Nycteridae.** With distinct cutaneous appendages on the margins of the apertures of the nostrils, with large united ears with well-developed tragi; the premaxillae are cartilaginous or small; upper incisors absent or small in the centre of the space between the canines; Ethiopian. Oriental. *Megaderma* E. Geoff., 2 sp. Asia, 2 sp. Afr., 1 sp. Australia; *M. lyra*, eat frogs and probably small mammals, India. *Nycteris* E. Geoff., Afr. 6 sp., Java 1 sp.

**Fam. Vespertilionidae.** Simple terminal nostrils without cutaneous appendages, ear with tragus, middle finger with 2 phalanges, with a long tail contained and produced to the hinder margin of the large interfemoral membrane;  $i \frac{2 \text{ or } 1}{3 \text{ or } 2} c \frac{1}{1} p \frac{3 \text{ or } 2}{3 \text{ or } 2} m \frac{3}{3}$ , molars with W-shaped cusps, upper incisors separated by a wide space and placed near the canines; 16 genera, and over 190 sp., in all temp. and trop. regions. *Antrozous* Allen, 1 sp., California. *Nyctophilus* Leach, 3 sp., Australasia. *Synotus* Keys. and Blas.,  $i \frac{2}{3} c \frac{1}{1} p \frac{2}{2} m \frac{3}{3}$ , 2 sp., *S. barbastellus*, the barbastelle, Britain, Eur., and a Himalayan sp. *Plecotus* E. Geoff.,  $i \frac{2}{3} c \frac{1}{1} p \frac{2}{3} m \frac{3}{3}$ ; 3 sp., 2 of which are N. American; *P. auritus*, the long-eared bat of this country, ranging to India. *Euderma* Allen, 1 sp., California. *Otonycteris* Ptrs., 1 sp. Africa and Asia. *Vesperugo* Keys. and Blas.,  $i \frac{2 \text{ or } 1}{3} c \frac{1}{1} p \frac{2 \text{ or } 1}{2 \text{ or } 3} m \frac{3}{3}$ , cosmopolitan, over 70 species, includes the common bats of most countries; the British species are *V. serotinus*, the serotine bat; *V. noctula*; *V. leisleri* and *V. pipistrellus*, the pipistrelle. *Chalinolobus* Ptrs., 8 sp., Australian and Ethiopian. *Scotophilus* Leach, 12 sp., Ethiop., Orient. and Austr. Regions. *Nycticejus* Raf., 1 sp., Amer. *Atalapha* Raf., 9 sp., Amer., Sandwich and Galapagos Islands. *Harpiocephalus* Gray, 1 sp. Japan, 8 sp. from the Himalayas to the Malay Arch. *Vespertilio* Keys. and Blas.,  $i \frac{2}{3} c \frac{1}{1} p \frac{3}{3} m \frac{3}{3}$ , cosmopolitan, 50 sp., 4 of which are British; *V. bechsteini*, Bechstein's bat; *V. nattereri*, the reddish-grey bat; *V. daubentoni*, Daubenton's bat; *V. mystacinus*, the whiskered bat. *Kerivoula* Gray, 15 sp., Oriental, Ethiopian. *Thyroptera* Spix., 2 sp., S. Amer. *Myxopoda* A. M.-Edw., 1 sp., Madagascar. The last two genera have hollow suctional organs on the base of the pollex and on the soles of the feet. *Miniopterus* Bon., throughout the Eastern Hemisphere, 5 sp.

**Fam. Emballonuridae.** With truncated muzzle; without nose-leaf, with generally large, often united, ears; with short, sometimes minute tragi; the tail is partially free, either perforating the interfemoral membrane and appearing upon its upper surface or produced far beyond its posterior margin; the first phalanx of the middle finger is folded in repose toward the upper surface of the metacarpal bone; dentition variable. Tropical and sub-tropical regions of both hemispheres.



Sub-fam. 1. **Emballonurinae**. Tail perforating the interfemoral membrane and appearing on its upper surface or terminating in it; legs long; upper incisors weak. *Furia* F. Cuv., 1 sp., Brazil. *Amorphochilus* Ptrs., 1 sp., Peru. *Emballonura* Temm., 7 sp., Madagascar, Malay Arch. *Coleura* Ptrs., 2 sp., S.-E. Afr., Seychelles. *Rhynchonycteris* Ptrs., 1 sp., Neotrop. *Saccopteryx* Illig., 7 sp., Neotrop. *Taphozous* E. Geoff., 11 sp., Ethiop., Orient. and Aust. Regions. *Diclidurus* Wied., 2 sp., Neotrop. *Noctilio* L., first upper incisors close together, giving a rodent-like appearance, feed on fish, 2 sp., C. and S. Amer. *Rhinopoma* E. Geoff., 1 sp., from Egypt through Asia Minor to India and Burmah.

Sub-fam. 2. **Molossinae**. Tail thick, produced far beyond the posterior margin of the interfemoral membrane (except in *Mystacina*); legs short and strong, with large feet, of which the first toe and often the fifth are much larger than the others, the feet are free from the wing membrane; of all bats the most fitted for terrestrial progression. *Molossus* E. Geoff., 10 sp., neotrop. *Nyctinomus* E. Geoff., 32 sp., trop. and warmer temp. zones of both hemispheres. *Mystacina* Gray, 1 sp., N. Zealand.



FIG. 327.—Head of *Vampyrus spectrum* (Régne animal).

Fam. **Phyllostomidae**. With cutaneous processes either surrounding or close to the nostrils; with moderately large ears and well-developed tragi; with 3 phalanges in the middle and 1 phalanx in the index finger; and with generally well developed united premaxillae; dentition variable. This family includes insectivorous, frugivorous, and blood-sucking forms. Confined to the Neotropical Region; 36 genera.

Sub-fam. 1. **Natalinae**. *Natalus* Gray, 3 sp.

Sub fam. 2. **Mormopinae**. Nostrils terminal, opening by simple apertures, not margined by a distinct nose-leaf; chin with expanded leaf-like appendage. *Chilonycteris* Gray, 6 sp. *Mormops* Leach, 2 sp.

Sub-fam. 3. **Phyllostominae**. Nostrils opening on the upper surface of the muzzle, and surrounded by a nose-leaf; chin with warts. *Lonchorhina* Tomes, 1 sp. *Macrotus* Gray, 3 sp. *Macrophyllum* Gray, 1 sp. *Vampyrus* E. Geoff., insectivorous and frugivorous, 2 sp.; *V. spectrum* L. (Fig. 327), which was supposed to be a blood-sucker, is mainly frugivorous. Other genera are, *Lophostoma*, *Schizostoma*, *Glyphonycteris*, *Trachyops*, *Phylloderma*, *Phyllostoma*, *Tyllostoma*, *Mimon*, *Carollia*, *Rhinophylla*, *Glossophaga*, *Phyllonycteris*, *Monophyllus*, *Ischnoglossa*, *Lonchoglossa*, *Anura*, *Choeronycteris*, *Lichonycteris*, *Artibeus*, *Vampyrops*, *Chiroderma*, *Stenoderma*, *Ectophylla*, *Ametrida*, *Pygoderma*, *Sturnira*, *Brachyphylla*, *Centurio*.

The true blood-suckers or *vampires* belong to this sub-family. They are *Desmodus* Wied. (2 sp.), without molar teeth and calcar, and *Diphylla* Spix. (1 sp.), with a small molar in each jaw and small calcar. The dentition is  $i \frac{1}{2} c \frac{1}{1} p \frac{2}{3} m \frac{1}{1} \frac{0}{0}$ , the upper incisors are large, canine-like and trenchant, the oesophagus very narrow, and

the cardiac end of the stomach produced into a long narrow caecum. They are small bats and suck the blood of men, horses and cattle and probably of other warm-blooded animals.

### Order 21. PROSIMIAE.\* (LEMUROIDEA).

*Plantigrade, usually pentadactyle, arboreal animals with opposable pollex and hallux. The orbit is closed behind by a bar of bone formed by the union of the frontal and jugal, but is not completely shut off from the temporal fossa by a wall. Digit No. 2 of the pes always has a claw.*

The lemurs are small or medium-sized, for the most part nocturnal animals, covered with fur and usually provided with a long tail which is never prehensile. They are generally quadrupedal, and the pollex and hallux are always well developed and opposable.

The dentition varies in the different families so that no general formula can be given for it, but except in *Chiromys*, which has no canines, all kinds of teeth are present. In living species it is usually  $i \frac{2}{2}$   $c \frac{1}{1}$   $p \frac{2 \text{ or } 3}{2 \text{ or } 3}$   $m \frac{3}{3}$ , but in some of the extinct forms attributed to this group from the Eocene and L. Miocene it is  $i \frac{3 \text{ or } 2}{3 \text{ or } 2}$   $c \frac{1}{1}$   $p \frac{4}{4}$   $m \frac{3}{3}$ , the teeth extending without a break along the jaw. The molars are tri- or quadri-tubercular, and the cusps are connected by low ridges. The third lower molar usually has a small talon. The premolars are always simpler than the molars, and have one sharp cusp, but the last may be molar-like.

The brain case is small relatively to the size of the face, which is generally elongated. The orbits, though completed behind by the bony union of the jugal and frontal are not completely shut off from the temporal fossa as in apes, nor does the lateral plate of the ethmoid enter into the inner wall of the orbit but is shut off by the maxilla. The lacrymal foramen is on the

\* Mivart, *Crania and Dentition of Lemuridae*, *P.Z.S.*, 1864 and 1867. Mivart and Murie, *Anatomy of Lemuroidea*, *Trans. Zool. Soc.*, 7, 1872. Turner, *Placentation of Lemurs*, *Phil. Trans.*, 166. A. Milne-Edwards, *L'embryol. d. Lemuriens et les affinités de ces animaux*, *Ann. Sci. Nat.*, 1871, and *Classification des Lemuriens*, *Revue Scientifique*, 1871. A. Milne-Edwards and Grandidier, *Hist. Nat. de Madagascar, Mammifères*, 1 and 2, 1875-96. Winge, *Primates*, *E. Museo Lundii*, 1895. Schlosser, *op. cit.*, see under *Carnivora*. Wortman, *Studies of Eocene Mammalia in the Marsh Collection*, *American Journal of Science*, 15, 1903, pp. 163, 399, 419. Hubrecht, *The Descent of the Primates*, New York, 1897.

face. It has been asserted that the Madagascar lemurs differ from others by the fact that the tympanic bone is reduced to a ring, and the bulla is formed by the periotic (F. Major, *P.Z.S.* 1899, p. 987).

The hind-legs are always longer than the fore. The humerus has an entepicondylar foramen and the femur a small third trochanter. The carpus usually has a centrale, and in some living species the tarsus is extraordinarily elongated (*Tarsius*, *Galago*, etc.), the elongation implicating the navicular and

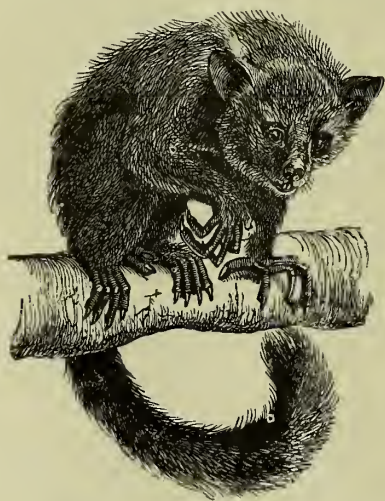


FIG. 328.—*Chronomys madagascarensis*  
(from Vogt and Specht).



FIG. 329.—*Galago (Otolemur) galago*  
(from Vogt and Specht).

calcaneum. In the pes, digit No. 2 often differs from the others in size and always bears a claw-like nail; while in the manus, digit No. 2 may be vestigial (*Potto*).

The cerebral hemispheres\* are relatively small and do not completely cover the cerebellum (except in the *Indrisinæ*). Their surface is only feebly convoluted, but the calcarine sulcus is indicated.

\* Flower, *Trans. Zool. Soc.*, 1863, p. 130. Beddard, *P.Z.S.*, 1895, p. 142. Oudemans, *Verh. Ak. Amsterdam*, 27, 1890.

There are no air-sacs or cheek-pouches. There is often a *sublingua*. The stomach is simple, the caecum large but without vermiform appendix. In many forms the arteries and veins break up into retia mirabilia as in some edentates and cetaceans.

The uterus is bicornuate and the placentation diffuse and nondeciduate (except in *Tarsius*). There is a scrotum, and the penis is pendent and usually has a bone. The urethra traverses the clitoris. There are usually a pair of mammae on the thorax, but there may be in addition one or two pairs on the abdomen.

The lemurs are frugivorous or omnivorous animals and are all arboreal. Most of them are nocturnal. There are about 50 living species, 35 of which are confined to Madagascar and to neighbouring islands. The rest are found in Africa and the Oriental region.

The sub-order dates from the Lower Eocene of Europe and America, but no representatives of living families are known earlier than the Pleistocene.

Fam. 1. **Lemuridae**. Dentition usually  $i \frac{2}{2} c \frac{1}{1} p \frac{2}{2} \text{ or } \frac{3}{3} m \frac{3}{3}$ ; upper incisors two on each side, vertical, small and separated by an interval in the middle line; upper canines are canine-like and projecting; lower incisors close-set, laterally compressed, proclivous, and the canines are closely applied to them and similar in form and direction. Premolars sharp, usually with one cusp, but the last may be molar-like.  $P 1$  on the lower jaw is canine-like, but bites behind the upper canine. Molars with three or four sharp cusps, connected by low ridges. The orbit is closed, but not shut off from the temporal fossa. The digits of both manus and pes, except digit 2 of the pes which has a claw, have flat nails; both pollex and hallux are opposable.

Sub-fam. 1 **Indrisinae**.  $i \frac{2}{1} c \frac{1}{1} p \frac{2}{2} m \frac{3}{3}$ ; milk dentition  $i \frac{2}{3} c \frac{1}{1} m \frac{3}{3}$ ,  $dm 1$  not being replaced; digits 2-5 of the pes united by a membrane as far as the end of the first phalanx; tail variable, pinna usually small. The hind-limbs are greatly developed, and when on the ground they walk on their hind legs, holding their arms above their heads. Colon spirally coiled, caecum large. Two pectoral mammae. Herbivorous. Confined to Madagascar. *Indris* Geoff., with moderate ears and reduced tail, carpus without centrale, upper incisors sub-equal, upper canine larger than  $p 1$ , 1 sp. *Propithecus* Benn., short ears, long tail, a centrale in carpus, outer upper incisor smaller than the inner, upper canine larger than  $p 1$ , 4 sp. *Avahis* Jourd., ears small, tail long, no centrale in carpus, outer upper incisors larger than inner, upper canine and  $p 1$  almost equal, 1 sp.

Sub-fam. 2. **Lemurinae**. Dentition usually  $i \frac{2}{2} c \frac{1}{1} p \frac{2}{3} m \frac{3}{3}$ ;



the lower canine and incisors are proclivous; upper incisors sometimes absent or only one pair. With long tails; toes of <sub>2</sub>pes not webbed; tarsus only slightly elongated. Caecum moderate. Confined to Madagascar and the Comoro Islands. *Lemur* L., face elongated, large ears, long tail, two pectoral mammae, upper incisors separated from each other and the canine; omnivorous, they carry their young; 8-15 species. *L. catta*, the ring-tailed lemur, less arboreal than other lemurs, often living among rocks and bushes. *Hapalemur* Gray, upper incisors very small, with 4 mammae, 2 sp. *Lepidolemur* Geoffr., upper incisors absent or reduced, 7 sp. *Mixocebus* Pet., upper incisors one pair, 1 sp.

Sub-fam. 3. **Galaginae**. Dentition as in last; the calcaneum and navicular are elongated, with large ears, long tail; with 4 mammae, 2 pectoral and 2 abdominal; Madagascar and Africa. *Chirozale* Geoffr., last upper premolar small, with only one external cusp, Madagascar, 4 sp. *Otolemur*, Madagascar, 2 sp.; both these genera sleep during the dry season, consuming fat which has been deposited at the root of the tail. *Galago* Geoffr., last upper premolar with two external cusps, nearly as large as *m* 1, Africa, 6 sp. *Microcebus* the smallest of lemurs, Madagascar.

Sub-fam. 4. **Lorisinae**. Slow lemurs; nocturnal, sluggish, with rounded head, large eyes, short ears, omnivorous. Dentition as in *Lemurinae*; digit No. 2 of the manus reduced and nailless; limbs nearly equal in length; tarsus not elongated; hallux directed backwards; tail reduced; two pectoral mammae; the arteries of the limbs form retia mirabilia as in sloths; African Continent and Oriental region. *Nycticebus* Geoffr., digit No. 2 of the manus small but complete, first upper incisor larger than the second, which often falls out early, no tail, 1 sp., Oriental region; *N. tardigradus*. *Loris* Geoffr., manus as in last, upper incisors small and equal, no tail, slender body and limbs, 1 sp., Oriental. *Perodicticus* Bennett, digit No. 2 of manus as a tubercle without nail, tail short, 1 sp., *P. potto*, Africa. *Arctocebus* Gray, manus as in last, 1 sp., Old Calabar.

*Megaladapis* F. Maj. (*Phil. Trans.* 1894) is a recently extinct gigantic lemur from the Pleistocene of Madagascar, about 4 times the size of a cat.

Fam. 2. **Tarsiidae**.\* With large eyes and ears, long thin tail tufted at the end, very long tarsus, fingers and toes ending in flattened discs, feeds on insects and lizards, arboreal;  $i \frac{2}{1}$   $c \frac{1}{1}$   $p \frac{3}{3}$   $m \frac{3}{3}$ ; inner upper incisor large and in contact with its fellow; molars with numerous pointed cusps; lower canine upright and diverging from the incisor. Orbit largely separated by a partition from the temporal fossa. Fibula united below with tibia; digits 2 and 3 of the pes with claws; other digits with nails. Calcaneum and navicular much elongated. Colon short, not folded. Placenta metadiscoidal, deciduate. Indo-Malaya Archipelago and Phillipines, 1 sp., *Tarsius spectrum*.

Fam. 3. **Chiromyidae**.† A squirrel-like animal with large ears, long bushy tail, inguinal mammae, digit No. 3 of manus thin and long, all digits with claws except the opposable thumb and hallux; it appears to

\* *Tarsius* is included by Hubrecht among the Primates, on account of its placenta (*Gegenbaur's Festschrift*, 2, 1896, p. 147).

† Oudemans, *Verh. Ak. Amsterdam*, 27, 1890.

feed on the juices of the sugar-cane, etc., on fruit, and on wood-boring caterpillars which it gets at with its rodent-like incisors, and then picks out with its thin finger, but the use of the latter is not clear; nocturnal and difficult to observe, makes a nest in trees. Dentition  $i \frac{1}{1} c \frac{0}{0} p \frac{1}{0} m \frac{3}{3}$ ; incisors large, rodent-like, with enamel on front only, with persistent pulps; grinding teeth with flat, faintly tuberculated crowns; milk dentition  $i \frac{2}{2} c \frac{1}{0} m \frac{2}{2}$ . One genus and species, *Chiromys madagascariensis*, the aye-aye, Madagascar.

A large number of extinct lemurs are known from the Eocene of Europe and N. America, but their remains have not been found, with the exception of one or two species in the Lower Miocene, in the formations intervening between the Eocene and the Pleistocene. The following may be mentioned, *Anaptomorphus* Cope, *Omomys* Leidy, *Mixodectes* Cope, *Necrolemur* Filhol, *Microchoerus* Wood, *Adapis* G. Cuv., *Caenopithecus* Rüt., *Pelycodus* Cope, *Hyopsodus* Leidy, *Indrodon* Cope, *Plesiadapis* Gerv., *Protoadapis* Lemoine. The remains are not complete, but the dentition appears to have been sometimes slightly reduced ( $i \frac{2}{2-0} c \frac{1}{1} p \frac{3-2}{3-2} m \frac{3}{3}$ ), and sometimes normal and in closed series, e.g. *Lemuravus*, *Pelycodus* ( $i \frac{3}{3} c \frac{1}{1} p \frac{4}{4} m \frac{3}{3}$ ), or in *Adapis*  $i \frac{2}{2} c \frac{1}{1} p \frac{4}{4} m \frac{3}{3}$ . Some of them had an entepicondylar foramen in the humerus, and a third trochanter on the femur. In *Anaptomorphus* and *Necrolemur* the cranial cavity is known to have been capacious; these two genera have been referred to the Tarsiidæ. Many of these forms while agreeing with lemurs in their skull (orbit, lacrymal foramen in front of orbit, etc.) resemble the apes more closely in the form of their dentition, and in the case of some of them there has been considerable difficulty in deciding whether they should be referred to the Insectivora, the Rodentia, or to the Lemuroidea. *Chriacus*, which was at one time held to be a lemur, is now placed with the creodonts, while *Mixodectes*, *Plesiadapis*, and *Protoadapis* have been referred to the Rodentia. As might be expected from the imperfection of the remains, the whole subject is in considerable confusion, and we can draw no satisfactory conclusions as to the nature and affinities of these early forms.

#### Order 24. PRIMATES.\*

*Plantigrade, usually pentadactyle animals with complete dentition,  $i \frac{2}{2}$ , bunodont premolars and molars, and two thoracic mammae. The orbit is completely separated from the temporal fossa, the pollex when present is always opposable (except in the Hapalidae). The cerebral hemispheres completely or almost completely cover the cerebellum, the uterus is without horns and the placentation is metadiscoidal.†*

\* H. O. Forbes, *Handbook to the Primates*, 2 vols., 1894 (Allen's Naturalist Library). Is. Geoffroy St. Hilaire, *Catalogue méthodique des Primates du Muséum de Paris*, 1851. Gray, *Catalogue of Monkeys, etc., in the Brit. Museum*, 1870. Schlegel, *Muséum d'Histoire Nat. des Pays Bas*. L. 12, Simiæ, 1876. Reichenbach, *Die vollständige Naturgeschichte der Affen*, 1863. Wortman, *Amer. Journal of Science*, 16, 1903, p. 345; 17, 1904, pp. 23, 133, 203.

† The placentation is at first diffuse; it becomes secondarily discoidal

The Primates include the Monkeys, Apes and Man. With the exception of the last named they are all well covered with hair, inhabit for the most part the warmer regions of the Old and New World, and are on the whole arboreal in habit. The baboons (*Papio*), however, inhabit rocky mountain regions. The most important characters are stated in the definition. In addition to those the following may be mentioned. The incisors are never more than  $\frac{2}{2}$ ; the canines are  $\frac{1}{1}$  and generally project; the upper molars have generally 4 cusps, but the posterior inner cusp may be weak or, in the American monkeys, absent; the lower molars are tetracuspitate, but the last usually has a talon (rarely present in the New-World forms). In the Old-World monkeys the molars usually increase in size from before backwards\*; in the New-World forms they diminish, the last being usually the smallest. The premolars have two cusps. There is generally a small gap between the incisors and canines particularly in the upper jaw.

The cranial cavity is spacious, and with the increase of the brain the cranial capsule becomes rounder and the foramen magnum gradually moves from the posterior part on to the lower surface. The orbits look forward and are always completely shut off from the temporal fossa, by the backward and inward extension of the postorbital processes of the frontal and jugal to meet the alisphenoid; the lacrymal foramen is intraorbital. In most of them the two frontals meet ventrally over the presphenoid between the ethmoid and orbitosphenoid, but this does not happen in *Homo*, *Simia*, *Anthropopithecus* and some *Cebidae*. The mastoid portion of the petiotic appears on the surface between the squamosal and exoccipital, but does not form a process except in *Homo*. The stylohyal is never ossified except in *Homo* and occasionally in *Simia*, and the tympanohyal is very small or absent.

The vertebrae are C7, D11-14, L4-7, S2-6, and caudal variable.

A clavicle is always present. The humerus never has an by the restriction of the villi to a discoidal area. In the discoidal type of placenta the placentation is discoidal from the beginning, and the chorion does not surround the embryo, but is confined to a discoidal patch.

\* In *Homo* and some other genera of the Anthropomorphidæ, the last molar is smaller than the others.

entepicondylar foramen, and the radius and ulna are separate and capable of pronation and supination. The carpus generally has a centrale (absent in *Homo*, *Gorilla* and *Anthropopithecus*), and the thumb is always opposable when present; it is occasionally absent.

The femur has no third trochanter; the tibia and fibula are separate, and the astragalus has a convex tibial surface with a lateral process for the fibula. The hallux is shorter than digit No. 2, and is opposable, except in *Homo*. The digits always have flat nails except in the *Hapalidae*.

The cerebrum is large and its surface is usually well convoluted (except in a few American monkeys); it completely or nearly completely covers the cerebellum. The lateral ventricle has a posterior cornu and hippocampus minor.

The uterus is without cornua. There is one pair of pectoral mammae, and the clitoris is not perforated by the urethra.

As already stated, most apes are arboreal and inhabit the forests of the warmer countries. Only a few lead a solitary life. Most of them live together in large companies which are led by the largest and strongest male. They feed chiefly on fruit and seeds, but also on insects, eggs and birds. The female produces only one young (rarely two or three) at a birth, and they protect and tend their offspring with great affection. Intellectually the apes take with the dog and elephant the highest place among mammals after man.

There are four families. Two of these, the *Hapalidae* and *Cebidae*, are confined to the New World, and are sometimes grouped together as the *Platyrrhina*; the other two, *Cercopithecidae* and *Anthropomorphidae*, are, with the exception of one genus (*Homo*), found exclusively in the Old World, and are sometimes grouped together as *Catarrhina*. The only European monkey is the Barbary ape (*Macacus inuus*), which is found on the precipices of Gibraltar.

The *Platyrrhina* are distinguished by possessing a broad cartilaginous internasal septum, by the absence of a bony external auditory meatus, and by the fact that the alisphenoid usually meets the parietal on the side of the skull, and the jugal joins the parietal. They are without cheek pouches and ischial callosities; the last lower molar is usually without a talon and



the last molar in both jaws is smaller than the preceding molar. In many of them the tail is prehensile.

In the Catarrhina the internasal septum is narrow, there is a bony external auditory meatus, the frontal usually meets the squamosal in the side wall of the skull (not in *Simia*), and the jugal does not join the parietal. The tail is never prehensile.

The Cebidae are found fossil in the Eocene. The other families, including the Anthropomorphidae, are first found in the Miocene.

Fam. 1. **Hapalidae.** Marmosets. Dentition  $i \frac{2}{2} c \frac{1}{1} p \frac{3}{3} m \frac{2}{2}$ ;

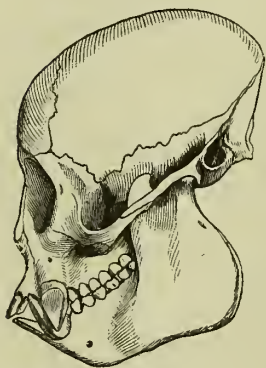


FIG. 330.—Skull of *Pithecia satanas* (from Claus).

upper molars tritubercular, the inner cusp being V-shaped; upper premolars broader than long with pointed inner and outer cusp; lower molars with four cusps,  $m 2$  is the largest in both jaws; canines projecting. The skull is rounded and the brain case capacious. The fore-limbs are shorter than the hind-limbs. All the digits have claws except the very small hallux, which has a nail, and the pollex is not opposable. The tail is longer than the rest of the body and is not prehensile. Cheek pouches and ischial callosities are absent; the ears are large and hairy. The cerebrum is large and has a smooth surface; there is a posterior cornu, a hippocampus minor and a deep calcarine fissure. There are no cheek pouches. They are frugivorous and insectivorous, and arboreal; and they give birth to three

young at a time. They are confined to the Neotropical Region. *Hapale* Ill., the lower canines are approximated to the incisors and do not exceed them in length; about 7 species. *Midas* Geoffr., lower canines longer than incisors, about 24 sp.

Fam. 2. **Cebidae.** These are also habitually quadrupedal, but the thumb is opposable as well as the hallux and the manus is a hand. All the digits of both limbs have nails. Dentition  $i \frac{2}{2} c \frac{1}{1} p \frac{3}{3} m \frac{3}{3}$ ; upper and lower molars tetracuspidate, premolars bicuspidate. The brain case is rounded and smooth; there is no mastoid process and the styloid process is not ossified. The skull varies considerably in the length of the face and the position of the foramen magnum. In *Mycetes* which represents one extreme the face is prominent and the plane of the foramen magnum posterior and almost vertical. In *Chrysotrux*, at the other extreme, the face is less prominent, the brain case arched, and the foramen magnum is on the under side of the skull, near its middle. There is a centrale in the carpus; the pollex is reduced to its metacarpal in *Ateles*. The tail is almost always long and prehensile; the ears are rounded and bare; cheek pouches and ischial callosities are absent. The stomach is simple, the caecum large, without vermiform appendix. The brain is

variable; in *Chrysothrix* the cerebrum projects behind the cerebellum, while in *Mycetes* it barely covers it; in *Cebus* and *Ateles* its surface is much convoluted, in others (e.g. *Nyctipithecus*) it is almost smooth. They are arboreal animals and confined to the Neotropical region. A few fossil remains of living forms have been found in the Pleistocene of Brazil and a few genera (*Homunculus*, *Anthropops*, *Pitheculus*) have been recorded by Ameghino from the Eocene of Patagonia, the family being unrepresented in the intermediate strata.

Sub-fam. 1. **Mycetinae**. Lower incisors vertical, hyoid bones inflated, tail long, prehensile and naked beneath at the end; pollex well developed. *Alouata* Lacép. (*Mycetes* Ill.), howling monkeys, face large with a low facial angle, the basicranial axis is as long as the cerebral cavity and the foramen magnum is placed at the hind end of the skull; the cerebrum is well convoluted, but it hardly covers the cerebellum; the rami of the mandible are very deep and protect the much swollen body of the hyoid in which is placed a large air sac communicating with the larynx below the epiglottis; the ventricles of the larynx are also dilated and prolonged upwards. They are in the habit of occasionally sitting on the topmost branches of trees and howling, the resonating apparatus increasing the power of the howls. The use of the howl is not known; it has been suggested that it is for the purpose of intimidating their enemies; 6 sp.

Sub-fam. 2. **Pitheciinae**. Lower incisors inclined forwards, tail not prehensile, pollex well developed. *Pithecia* Geoffr., the sakis, with long tail, 5 sp. *Brachyurus* Spix (*Ouacaria* Gray), short tail, 3 sp., which have a curious and local distribution in the forests on the banks of the Amazon.

Sub-fam. 3. **Nyctipithecinae**. Lower incisors vertical, tail long, not prehensile, pollex well developed. *Callithrix* Geoffr., teetees, about 11 species. *Chrysothrix* Kaup; squirrel monkey, face small with high facial angle, plane of the foramen magnum horizontal, cerebrum nearly smooth, projecting behind the cerebellum, 3 sp. *Nyctipithecus* Spix, douroucoulis, nocturnal, with large eyes, with owl-like face, head and brain as in the last; 5 sp.

The extinct Eocene genera of Ameghino, *Homunculus*, *Anthropops*, *Pitheculus*, *Homocentrus*, *Eudiastatus*, are placed in this sub-family.

Sub-fam. 4. **Cebinae**. Lower incisors vertical, tail long, prehensile, pollex may be absent. *Ateles* E. Geoffr., spider-monkeys, coaitas, slender, long limbed forms with non-woolly fur, and absent pollex; tail naked below at the end, very prehensile; about 11 sp. *Brachyteles* Spix (*Eriodes* E. Geoffr.), with woolly fur and reduced pollex, tail naked below at the end, nails compressed and pointed; 3 sp. *Lagothrix* E. Geoffr., barrigudos, woolly monkey, pollex well developed, tail naked below at the end, fur woolly; 2 sp. *Cebus* Erxleb., sapajous or capuchins, monkey of organ grinders, not woolly, pollex well developed, tail completely hairy; about 17 species.

The extinct family **Nesopithecidae** from the Pleistocene of Madagascar is placed here. It has also been assigned to the lemurs. The lacrymal foramen is just inside the orbit, and the dentition is  $i \frac{2}{2} c \frac{1}{1} p \frac{3}{3} m \frac{3}{3}$ , the molars being pitheciine, but the tympanic bulla is formed by the periotic as in Madagascar lemurs.

Fam. 3. **Cercopithecidae.** These Old-World monkeys are essentially quadrupedal, and the hind limbs are not much longer than the fore-limbs. Both pollex (when present) and hallux are opposable, and they usually have a tail which is never prehensile. Ischial callosities are present; cheek-pouches present or absent. All the digits of both limbs have nails. Dentition  $i \frac{2}{3} c \frac{1}{1} p \frac{2}{2} m \frac{3}{3}$ ; molars elongated antero-posteriorly, usually tetracuspidate, last lower molar often with a talon; the outer and inner pairs of cusps are sometimes separated by a longitudinal furrow and sometimes connected by transverse ridges; premolars bicuspidate. The skull varies in shape, the frontal region being rounded and the facial angle small, or the face is prolonged and dog-like and the facial angle is large. The nasal septum is narrow. There is no distinct mastoid process, and the styloid process is not ossified; the parietals do not unite with the alisphenoid, being cut off by the union of the squamosal and frontal. There is a bony external auditory meatus. The frontal bones usually unite across the base of the skull in front of the union of the presphenoid and ethmoid; the basicranial axis is shorter than the length of the cerebral cavity, and the foramen magnum looks obliquely backwards and downwards. The suture between the premaxillary and maxillary bones does not disappear until the permanent dentition is complete. The carpus has a centrale, and the pollex is complete except in *Colobus*. The posterior ends of the ischia are everted and rough. The stomach is usually simple, the caecum small and without a vermiform appendix. A median air-sac is sometimes present opening into the larynx below the epiglottis: it may be large, extending down the neck and sending processes into the axilla. The brain is large, the cerebrum projects behind the cerebellum, and its surface is always complexly convoluted. The penis usually has a bone. The phenomena of oestrus appear to approximate to those found in the human female.\* They are confined to the Old-World, being found in the Ethiopian (absent from Madagascar), Oriental, and Palaearctic regions. The fossil remains are few, but representatives of living genera are found as far back as the Pliocene; and a few genera classed with existing families are known from the Pliocene and Miocene of Europe.

Sub-fam. 1. **Cercopithecinae.** Omnivorous, with cheek-pouches, simple stomach; fore- and hind-limbs sub-equal, nostrils terminal, tail long, short or absent. *Papio* Erxl. (*Cynocephalus* Lacép.), African baboons; muzzle elongated, dog-like, and tail moderate, ischial callosities large; they usually inhabit rocky ground and are frequently gregarious; about 9 living species, Africa and Arabia, and a few extinct from the Pliocene and Pleistocene of India and the Pleistocene of Algeria; *P. maimon*, mandrill, tropical W. Africa; *P. porcarius*, chaima, S. Afr. *Theropithecus* I. Geoffr., like the last, but nostrils sub-terminal, 2 sp., Abyssinia. *Cynopithecus* I. Geoffr., 1 sp., the black ape of Celebes. *Macacus* Lacép., muzzle produced, nostrils not terminal, tail long, short or absent; last lower m. with talon; generally gregarious; about 20 sp., all Asiatic except *M. inuus*, the Barbary ape of N. Afr. and Gibraltar, without tail; *M. rhesus*, the Bengal monkey; *M. speciosus*, Japan, the most northerly monkey and the only one found in Japan. *Cercocebus* E. Geoffr., mangabeys, like *Cercopithecus*, but last lower molar with talon; long tail, upper eyelids white, 6 sp., W. Afr. *Cercopithecus*

\* Heape, *op. cit.*, p. 517.

Erxl., guenons, muzzle shorter, ischial callosities moderate, tail long, last lower m. without talon; about 40 sp., Africa; *C. diana*, Diana monkey; *C. callitrichus*, green monkey; *C. lalandi*, the vervet. *Miopithecus* T. Geoffr., talapoin, like the last, but the lower molars have only 3 cusps.

The extinct *Oreopithecus* Gerv., from the Miocene of Italy, is included here.

Sub-fam. 2. **Semnopithecinae.** More purely herbivorous, without cheek pouches, with sacculated stomach, long tail; the build is slender and the hind limbs are longer than the fore. In the skull the frontal region is more rounded and the facial angle smaller than in the Cercopithecinae. The stomach is divided into 3 chambers, of which the middle is sacculated. *Semnopithecus* F. Cuv., langurs, with small pollex, and narial aperture extending upwards between the orbits; Asia, from the Himalayas (*S. schistaceus*) at 11,000 ft. to Borneo and Sumatra; about 29 sp. *S. entellus*, the sacred ape of the Hindoos. *Colobus* Illig., guerezas, pollex absent or reduced to a tubercle with or without a nail, arboreal, celebrated for their skins, 11 sp., Afr. *Nasalis* E. Geoffr., proboscis monkeys, the nose is produced into a proboscis in the adult, 1 sp., Borneo. *Rhinopithecus* A. M.-Edw., 1 sp., China.

The extinct *Mesopithecus* Wag., from the Miocene of Greece, and *Dolichopithecus* Dep. from the Pliocene of France are placed here.

Fam. 4. **Anthropomorphidae** \* (Simiidae). Erect or semi-erect animals. In the former case progression is effected entirely on the hind limbs; in the latter the anterior limbs, which are in this case longer than the posterior, may be used to assist in locomotion, the tips of the fingers or the knuckles being applied to the ground. The body is covered with hair, but in one genus (*Homo*) it is much reduced, especially on the back. The pollex is always and the hallux usually opposable, and all the digits, except in *Hylobates*, have flat nails. A tail is always absent. Cheek pouches are also absent, and ischial callosities except in *Hylobates*. Dentition  $i \frac{2}{2} c \frac{1}{1} p \frac{2}{2} m \frac{3}{3}$ , in closed series in *Homo*, but with a slight diastema between the incisors and canine in the other genera; the inner upper and the outer lower incisors are larger than the others; the canines project except in *Homo*; the molars have 4 cusps (except the 2nd lower molar, which has 5), the inner and outer alternating, without transverse ridges; the last lower molar with or without weak talon; upper premolars broader than long, bicuspidate. The skull varies, but in all the frontal region is well developed and the facial angle small. Supraorbital and occipital ridges are present in all except *Homo*. In *Hylobates* and *Anthropopithecus* the sagittal crest is absent, and the occipital (lambdoidal) small. The alisphenoids usually meet the parietal in *Hylobates*, *Simia* and *Homo*, but in *Anthropopithecus* and *Gorilla* they are cut off by the union of the frontal and squamosal. There is a bony external auditory meatus. The frontals meet in the base of the skull over the ethmopresphenoidal suture in *Hylobates* and *Gorilla*, but not in *Anthropopithecus*, *Simia* and *Homo*. The mastoid projects in *Homo*, but not in the other genera. There is no ossified styloid process,

\* Hartmann, *Anthropoid Apes*, Internat. Sci. Series, London, 1885. H. O. Forbes, *op. cit.* Huxley, *Man's Place in Nature*, London, 1894 (Collected Essays, vol. 7).



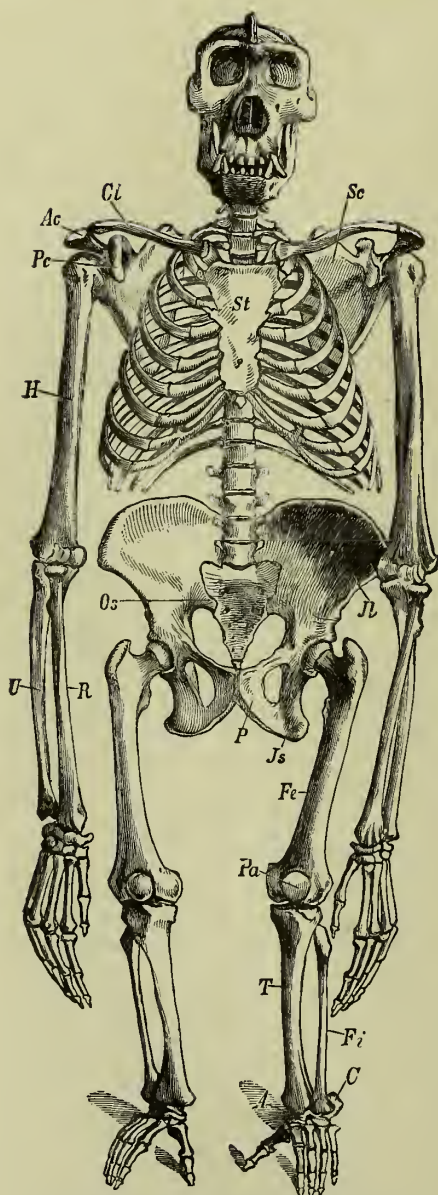


FIG. 331.—Skeleton of *Gorilla* (from Claus). — *A* astragalus, *Ac* acromion, *C* calcaneum, *Cl* clavicle; *Fe* femur, *Fi* fibula, *H* humerus, *Il* ilium, *Is* ischium, *Os* sacrum, *P* pubis, *Pa* patella, *Pe* coracoid process, *R* radius, *Sc* scapula, *T* tibia, *U* ulna.

except in man and occasionally the orang. The suture between maxillary and premaxillary bones disappears in man before birth, in the other genera it persists until the completion of the second dentition or nearly to that period. In *Hylobates* there are 18 dorsolumbar vertebrae, in *Simia* 16, but in the other genera the number is 17. *Homo* and *Simia* have 12 pairs of ribs, *Anthropopithecus* and *Gorilla* 13. The sacrum contains at least 5 ankylosed vertebrae. The carpus has a centrale in *Hylobates* and *Simia*, but not in *Anthropopithecus*, *Homo* or *Gorilla*. The hallux is opposable except in *Homo*. The cerebrum is always well convoluted and large, projecting back behind the cerebellum (except in the Siamang). The volume of the brain in *Simia* and *Anthropopithecus* is about half that of man; in *Gorilla* it is rather larger. The stomach is simple, and the caecum small with a vermiform appendix. There is an os penis except in *Homo*, in which there may sometimes be a trace of it. All are omnivorous, and all arboreal, except *Homo*.

A few fossil species belonging to existing genera are known from the Pliocene of India, and three fossil genera, *Pithecanthropus* Du Bois, from the Pliocene of Java, *Dryopithecus* Lartet, and *Pliopithecus* Gervais, from the Miocene of Europe.

*Dryopithecus* seems to have been allied to the gorilla and *Pliopithecus* to the chimpanzee. *Pithecan-*

*thropus* \* seems to have been nearer to *Homo*. The remains consist of a skull cap, two teeth and a femur, which are supposed to have belonged to the same individual. The cranial capacity was probably about two-thirds that of man, the forehead low, and the supraorbital ridges prominent. The femur indicates an upright gait.

*Hylobates* Ill., the gibbons. Arboreal. Body and limbs slender, fore limbs so long as to reach the ground when the animal is walking upright. The carpus has a centrale, the nails of the pollex and hallux are alone flat, and the hallux is well developed, and there are small ischial callosities. There are 18 dorso-lumbar vertebrae and 13 pairs of ribs. In walking they habitually go upright with the flat of the sole on the ground and without the assistance of the arms. Smaller than the other genera, height not exceeding 3 feet, S.E. Asia, 9 species; omnivorous. *H. syndactylus*, siamang, possesses a laryngeal sac, communicating with the larynx by two openings in the thyrohyoid membrane.

*Simia* L., the orang-utan, 1 sp., *S. satyrus* in Borneo and Sumatra; arboreal. Body and limbs massive, the fore-limbs reach to the ankle, the carpus has a centrale, the pollex and hallux are small, and the latter is sometimes without a nail; 16 dorsolumbar vertebrae and 12 pairs of ribs. The males attain a height of a little over four feet, and have a beard when adult. They walk on the outsides of their feet with their knuckles on the ground. There is a large median vocal sac ventral to the trachea which extends as far as the axilla; it communicates with each of the ventricles of the larynx. They build a nest on trees. Exclusively herbivorous.

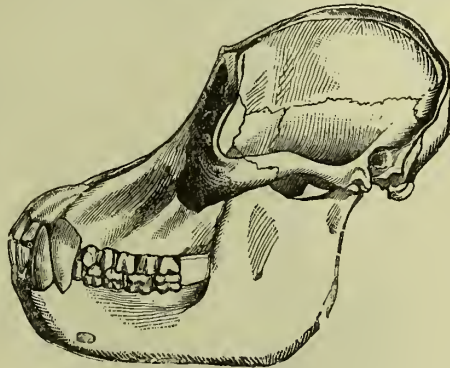


FIG. 332.—Skull of *Simia satyrus* (from Claus).

*Gorilla* I. Geoffr., 1 sp., *G. gorilla* in the forests of W. Africa; arboreal, but less so than the next genus; mainly herbivorous. Body and limbs massive, the fore-limbs reach to the middle of the lower leg, the carpus is without centrale, hallux well developed, 17 dorsolumbar vertebrae and 13 pairs of ribs. Male larger than female, with strongly developed ridges on the skull, and with larger canine teeth. The male may attain a height of  $5\frac{1}{2}$  feet. Their air-sacs are very similar to those of *Simia*. They walk like the chimpanzee on the soles of their feet with the backs of their hands on the ground. The heel is better developed than in *Simia*, and they can stand and walk without the assistance of their arms. They have a ferocious and gloomy disposition and are untameable.

*Anthropopithecus* de Blainville (*Troglodytes* E. Geoffr.) the chimpanzee, arboreal; 2 sp., *A. troglodytes* L., and *A. tchego* Duv., W. Africa. Very

\* Dubois, *Pithecanthropus erectus*, *Eine menschenähnliche Uebergangsform aus Java*, Batavia, 1894, and *Proceedings of the Zoological Congress at Leyden*, 1895.

similar to *Gorilla*, but the mandibular symphysis is shorter, the skull is without the sagittal crest and the males and females are very similar the former having larger canine teeth. Height does not exceed 5 feet. Vocal sacs as in *Gorilla*. Arms reach but a slight distance below the knee. They walk with the flat of their soles upon the ground, either with or without the support of their arms. They have a lively and comparatively gentle disposition and are tameable.



FIG. 333.—*Gorilla gorilla* (from Vogt and Specht).

*Homo* \* L., 1 sp., *H. sapiens* L., world wide in distribution. Fore-limbs shorter than the hind-limbs, the fore-limbs reaching a little below the middle of the thigh. The carpus is without a centrale. The hallux is

\* Darwin, *Descent of Man*, 2nd ed., London, 1885. Lyell, *The Antiquity of Man*, 4th ed., London, 1873. Huxley, *Evidence as to Man's Place in Nature*, *op. cit.* Quatrefages, *Hist. gén. des races humaine*, Paris, 1887-89. Flower, On the classification of the varieties of the human species, *Journ. Anthropol. Inst. Gt. Brit. and Ireland*, 1885. Fraipont and Lohest, La race humaine de Néanderthal ou de Canstadt, *Arch. Biol.*, 7, 1887, p. 587. Wiedersheim, *The Structure of Man*, etc., London, 1895. Schwalbe, *Die Vorgeschichte des Menschen*, 1904. W. L. H. Duckworth, *Morphology and Anthropology*, Pitt Press, 1904.



large but not opposable. There are seventeen dorso-lumbar vertebrae and twelve pairs of ribs. The canine teeth scarcely project in either sex ; there is no diastema ; and, as in *Simia*, the posterior molar is smaller than the others. The males usually have a beard. The legs are relatively longer than in the other genera. The hairy covering is much reduced, especially on the back. There are no vocal sacs. The brain is at least twice the size of the brain of *Simia* and *Anthropopithecus* and rather less than twice the size of *Gorilla*, but the convolutions though more complex are very similar. They walk erect on the soles of the feet.

The skull is without the sagittal and occipital crests and the supraorbital ridges are less strongly developed than in other Anthropomorphidae. The frontal development and the preponderance of the cranial over the facial part of the skull is more marked than in any other genus of the family, or indeed in any other Old-World Primate, but curiously enough some of the new-world forms, e.g. *Chrysothrix*, approach *Homo* in these points. The early disappearance of the suture between the maxilla and premaxilla, the projection of the nasal bones, the slight projection of the canines and the absence of a diastema in the tooth series are also distinctive human features. The foramen magnum looks almost directly downwards. The symphysis of the lower jaw has a mental prominence, an indication of which is seen also in *Hylobates*. They are omnivorous gregarious animals, being chiefly distinguished from the other genera of the family by the feebleness of the hairy covering, the non-opposable hallux and completely erect attitude, and by their larger brain. The latter feature is associated with the greater mental development, which is the especial characteristic of the genus. This shows itself in their speech, their more effective powers of reasoning, and in the intellectual qualities of sympathy and imagination, in virtue of which they have at last been able to dominate all other animals, to accommodate themselves to every climate, and to spread to every quarter of the globe.

Living men, though forming one species, fall into a considerable number of varieties or races. These pass imperceptibly into one another and it is impossible to construct a satisfactory classification of them. They are all, so far as is known, fertile with one another, and there can be no question that the intermingling which is thus rendered possible has been in the past a potent factor in giving rise to new races, and that it is taking place at the present day. It is a striking commentary on the attempts of modern naturalists to discover the pedigrees of different species of animals that, with our relatively full knowledge of man, historical, anatomical and ethnological, we are unable to agree upon a zoological classification of him which shall show the consanguinity of the different races. It has usually been the habit of anthropologists to establish certain primary groups or types of men presenting some variations within themselves and therefore divisible into sub-groups, and connected with each other by intermediate forms which have been produced by crossing. These primary groups are regarded as primitive or ancestral types from which all the extant races of men have been derived by descent with modification. It is therefore of the first importance to determine them. This however cannot be done for there is no agreement and apparently no possibility of agreement among naturalists ; and even if we give our adherence to any particular scheme, the difficulty remains of assigning to their proper places the intermediate races, which often present equally important resemblances to more than one of our primary types.



We therefore relinquish the attempt to ascertain the primary races, and we relinquish it without regret, for we doubt if any such natural groups exist or ever have existed in nature. They are useful groups for the student and as such have considerable value. But too much importance must not, in our opinion, be attached to them, for it cannot be shown that at any previous epoch in the history of man an interdigitation of races which is so characteristic of the present time did not exist.

The primary groups \* into which the human race may be divided are three in number: (1) the Negroid races, (2) the Mongolian, and (3) the Caucasian.

(1) The Negroid races are characterised by frizzly hair, dark skin, a broad flat nose, thick lips, prominent eyes, large teeth, a narrow pelvis, and dolichocephalic skulls. The typical example of this group is the African Negro. The following varieties may be mentioned: (a) the Bushmen of S. Africa; they have a yellowish skin and in certain other features approach the Mongolian type. (b) The Pigmy races of the Central African Forests, of the Andaman Islands, Malay Peninsula and the Philippines; they depart from the type in having brachycephalic skulls. (c) The Melanesians or Oceanic Negroes of the Western Pacific and the Tasmanians; they depart in many features from the type and are probably largely mixed with other races. (d) The Australians who differ in many respects from the type, notably in not possessing the frizzly hair.

(2) The Mongolian races have a yellowish skin, black straight hair, a broad face with prominent cheek bones, small nose, sunken narrow eyes, teeth of moderate size, and a variable skull. The typical examples of this group are the inhabitants of Northern and Central Asia (China, Thibet, Japan, Burmah and Siam). In Europe they are represented in a much modified form by the Lapps, the Finns, the Magyars and the Turks. The other representatives of this group are the Esquimaux, the Malay (including the inhabitants of Madagascar), the brown Polynesians (Samoan, Tongan, Eastern Polynesian Islands and New Zealand) who present in some respects affinities to the Caucasian group, and lastly the original inhabitants of the continent of America who differ in some important respects from the type.

(3) The Caucasian or White races, which present two main varieties, (a) the Xanthochroi with fair and white skin found in Northern Europe extending into North Africa and West Asia, (b) the Melanochroi with black hair and skins varying in colour from white to black. The Melanochroi comprise the inhabitants of S. Europe, N. Africa, and S.W. Asia. The Caucasians have soft, straight hair, well developed beard, variable cranium, retreating cheek-bones, narrow and prominent nose, small teeth, and broad pelvis.

Man is not known fossil till the Pleistocene. He is there represented by *H. sapiens*, and by an extinct species, *H. primigenius* Schwalbe (*neanderthalensis*) from the Neanderthal (1856), from Spy (1885), and from Krapina in Croatia (about 1899), and possibly from other localities. This extinct species is not thoroughly known, but it clearly belongs to a lower grade of organisation than *H. sapiens*.

\* In the following account the classification adopted by Flower and Lydekker (*op. cit.*) has been mainly followed.

The mental qualities which are so characteristic of the genus *Homo* have led many naturalists to create a special family (*Anthropidae*) or even order (*Bimana*) for its reception. But in this work we are concerned with man from the standpoint of morphology, and, in assigning him his position in the system, we can only take into consideration the facts of his bodily structure, as we have done in the case of other animals. If psychical characters were taken into account in Zoology, the whole of classification would be thrown into confusion, and in the case of man how should we define the position to be assigned to him? For

*What a piece of work is a man! How noble in reason!  
how infinite in faculty! in form and moving how express  
and admirable! in action how like an angel! in apprehension  
how like a god!*

and again

*Thou hast made him a little lower than the angels and  
hast crowned him with glory and honour.*

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